

THE SUBPHYLUM CALCICHORDATA
(JEFFERIES 1967)
PRIMITIVE FOSSIL CHORDATES WITH
ECHINODERM AFFINITIES



BY

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SYNOPSIS

The orders Cornuta (Jaekel 1900) and Mitrata (Jaekel 1918), which constitute the class Stylophora (Gill & Caster, 1960) (Cambrian to Devonian) and which are customarily placed in the Echinodermata, are transferred to the Chordata as the Subphylum Calcichordata (Jefferies 1967). With Gislén (1930), the Calcichordata are regarded as ancestral to the Urochordata, Cephalochordata and Craniata.

The cornutes *Cothurnocystis elizae* Bather and *C. curvata* Bather had external branchial slits in the left, dorsal part of the theca that were mechanically adapted as outlet valves. The mouth was near the anterior end of the theca. The anus, situated left of the stem, was external in *C. elizae* but opened into the most median gill slits in *C. curvata*. Anterior and posterior coeloms, pharynx and buccal cavity can be recognized in the theca. The stem, which is homologous with both the stem of a crinoid and the tail of a fish, had an anterior part for lateral flexion, a posterior part adapted for upwards flexion and a medial rigid part containing a ventral massive element, the stylocone. In the posterior stem evidence indicates the presence of segmental muscle blocks, a median chambered organ or notochord and probable paired segmental blood vessels. The brain or aboral nerve centre was at the anterior end of the stem.

The mitrates *Mitrocystella incipiens* (Barrande) *miloni* Chauvel and *Mitrocystites mitra* Barrande had paired, posterior gill openings and presumed, paired, internal gill slits. The mouth was at the anterior end of the body and pointed somewhat leftwards, particularly in juvenile *M. mitra*, like the mouth of larval amphioxus. Anterior and posterior coeloms, left and right pharyngeal chambers, buccal cavity and paired posterior atria can be recognized in the theca. The rectum opened into the left atrium as in a living tunicate tadpole. Left gill slits probably preceded right gill slits in ontogeny as in amphioxus. The stem, as in cornutes, had anterior, medial and posterior parts. The anterior part was probably adapted to lateral flexion, the medial part contained a massive dorsal element (styloid), and the posterior part was adapted for flexing downwards. In the posterior stem, evidence indicates the presence of segmental muscle blocks, notochord, dorsal nerve cord, paired segmental ganglia and a complicated vascular system. The brain was at the anterior end of the stem and was fish-like in

character with optic, hypophyseal, medullary and olfactory parts. The cranial nerves were complicated and included homologues of the trigeminal complex and trigemino-profundus ganglia and of the olfactory, optic and lateralis complexes of fish.

The extant chordate subphyla probably derived from a primitive, probably Upper Cambrian, mitrate that became free swimming.

The following homologies are suggested between chordates and crinoids: notochord = chambered organ; dorsal nerve cord = peduncular nerve; longitudinal vessel broadly = haemal strand; brain = aboral nerve centre; cranial nerves broadly = aboral nerves to theca.

Ubaghs' interpretation of the stem of Stylophora (1961b) is rejected as also is the classical theory of vertebrate head segmentation. Lindström's (1949) interpretation of the cranial nerves of cephalaspids is adopted as the most reasonable yet proposed.

I. INTRODUCTION

THE subjects of this paper are certain bizarre fossils, conventionally regarded as echinoderms, belonging to the orders Cornuta Jaekel 1900 and Mitrata Jaekel 1918. The conclusion is reached, with Gislén (1930), that, while having definite echinoderm affinities, they are better placed in the Chordata, and are the ancestors of other Chordata, including tunicates, Amphioxus and the vertebrates.

The Cornuta and Mitrata are conventionally regarded as members of Jaekel's Class Carpoidea 1900. This is usually defined as including the orders Cornuta, Mitrata, Soluta, Cincta and Digitata (e.g. Gill & Caster 1960 : 11). The extent to which the Carpoidea are a natural group is doubtful. It is certain, however, as shown below, that Cornuta and Mitrata are closely allied to each other. They were placed by Gill & Caster (1960 : 11) in the distinct Superorder Stylophora, here regarded as a class.

A relationship between echinoderms, hemichordates and chordates is widely accepted (p. 327). The suggestion that Cornuta and Mitrata are in fact chordates, and ancestral to other chordates, is therefore inherently plausible. It was mentioned in passing by Matsumoto (1929 : 27) and argued in detail, and with great erudition, by Gislén (1930). Gislén's views were mentioned favourably by Gregory (1935 : 280; 1936 : 321; 1946 : 358), Caster (1952 : 37), and Caster & Eaton (1956). They have not been widely accepted, however, mainly because Gislén's argument was based on embryology rather than fossils, and his reconstruction of the soft parts of cornutes and mitrates was little more than guesswork. Berrill (1955 : 5) dismissed Gislén's hypothesis in a paragraph. Marcus (1958 : 50), however, expressed the view that "Future evidence of the origin of the Chordata from the Carpoidea would by no means be surprising."

I agree with Gislén's broad results and with some of his major anatomical suggestions such as the position of the mouth in cornutes and mitrates and of gill slits in cornutes, the homology of carpoid stem and fish's tail, and the homology of some of the asymmetries of larval *Amphioxus* with those of mitrates and cornutes. Most of Gislén's detailed arguments, however, seem to be incorrect.

Other works dealing with the morphology of mitrates and cornutes generally agree on details but flatly disagree on essentials. Among the most important are Jaekel (1900; 1918), Bather (1913; 1928), Chauvel (1941) and Ubaghs (1961a; 1961b; 1963). Chauvel's reconstruction of the nervous system of *Mitrocystella* is

a *tour de force* and Ubaghs' observations on the details of stem structure are also highly important, though his conclusions are not acceptable.

The present work takes the form of a detailed morphological study of the cornutes *Colthurnocystis elizae* Bather and *C. curvata* Bather, and the mitrates *Mitrocystella incipiens* (Barrande) *miloni* Chauvel and *Mitrocystites mitra* Barrande. These forms were chosen because they are reasonably large (theca about 3 cm. across), well represented in the British Museum (Natural History) collections and preserved largely as hollow moulds, with the skeletal calcite dissolved away. This allows the internal mould to be examined direct and the form of the skeleton to be obtained by means of latex and dental rubber casts. The reconstructions, based on observations of as many specimens as possible, were drawn in several projections simultaneously on a drawing board. Supplementary observations were made on *Ceratocystis perneri* Jaekel, *Phyllocystis blayaci* Thoral, *P. crassimarginata* Thoral, *Chinianocarpus thorali* Ubaghs, *Lagynocystis pyramidalis* (Barrande) and *Peltocystis cornuta* Thoral.

In reconstructing the soft parts, a functional explanation has been sought for as many features as possible. It was assumed that the soft parts of the four species mainly studied were fundamentally the same. The fossils have been interpreted by analogy first with crinoids, and secondly with tunicate larvae and fish.

The results flatly contradict the idea of a completely segmented vertebrate ancestor with mandibular and premandibular gill slits which is so firmly embedded in classical vertebrate anatomy (e.g. Goodrich 1918) but for which the evidence is, in fact, very weak (Kingsbury 1926). They agree somewhat better with the views of students of tunicates such as Berrill (1955) and Garstang (1928), except that there is no evidence of neoteny. They also agree better with the account of cephalaspid cranial anatomy given by Lindström (1949) than with that of Allis (1931), Wangsjö (1952) or Stensiö (1927; 1958). Wangsjö's interpretations are preferable in many respects to Stensiö's but Lindström's seem more reasonable than either.

As regards nomenclature, the terms anterior, posterior, dorsal and ventral, right and left are used as for a fish. The plate nomenclature is a much modified version of that of Jaekel (1900). The nomenclature of Caster (1952) could not be used, since a scheme was needed that was applicable to both cornutes and mitrates and which was not too dependent on the correct homology of plates. The following notation is employed: C = a central dorsal plate of the theca, D = a dorsal plate of the anterior stem, M = a marginal plate, S = a ventral spike, V = ventral plate of theca, VS = ventral plate of stem, suffix _A = anterior, suffix _D = dorsal, suffix _L = left, suffix _R = right, suffix _V = ventral, suffix _{(0) 1, 2, 3} etc. indicates position in sequence counting from anterior end of stem.

A brief account of the work described in the present paper has already been published (Jefferies 1967), and in that work the name Calcichordata was used for the first time. Since writing that brief account I have changed my mind on some details. Thus the median line nerves of cornutes cannot represent the optic nerves (n_3) of mitrates since they pass ventral to the gut. They may possibly correspond to the nerves n_0 of mitrates. Again, the peripheral canals of *M. incipiens miloni*

probably did not extend forwards to open in the olfactory openings. Consequently the fibres of the olfactory nerves did not travel anteriorly in the peripheral canals, and did not have to leave these to reach the telencephalon. The reconstruction of the anterior parts of the nerves n_2 of *M. mitra* has been altered in some respects. Further it no longer seems likely, though it is still possible, that the Cephalochordata derived from a different group of mitrates to the Urochordata and Craniata. The probable position of the oesophagus of *M. i. miloni* and the probable ontogenetic origin of the posterior coelom of *M. i. miloni* and *M. mitra* were not discussed in the earlier paper. None of these are very important points and they do not affect the fundamental thesis here advanced.

II. ACKNOWLEDGMENTS

The author gratefully acknowledges the help of numerous colleagues. Dr. W. T. Dean initiated the investigation by finding a mitrate from Shropshire that he discussed with the author. Mr. H. G. Owen and Mr. A. E. Rixon have been very helpful in technical matters. Drs. Horný and Zazvorká of Prague, M. Mattei of Montpellier, Prof. Milon of Rennes, Dr. B. Kummel of Harvard and Prof. David of Lyon, have allowed specimens in their charge to be examined. Prof. J. E. Smith made available the facilities of the Marine Biological Station, Plymouth and Dr. D. B. Carlisle introduced me there to living tunicates. Innumerable colleagues have discussed the subject with the author, helping to clarify ideas, and making many suggestions. In this respect I would particularly like to mention Dr. E. I. White, M. J. Chauvel, Dr. R. Prokop, Dr. Q. Bone, Dr. G. Underwood, Dr. D. B. Macurda, Prof. J. Wyatt Durham, Dr. N. J. Holmes, Dr. M. H. Hey, Dr. C. Patterson and Dr. C. R. C. Paul. Prof. Ubaghs gave the author the chance to see much unpublished work. Our agreement on facts was combined with almost complete disagreement on interpretation. Mr. P. Minton generously gave several afternoons to discussion and made numerous helpful suggestions on functional morphology from an engineer's standpoint. Text-figures 1a, b; 2; 4b, d; 6; 8a, b; 11a; 13a, b, 14a, b; 17b; 19a; 20; 21; 23a, b; and 27a are reproduced here by kind permission of the Zoological Society of London.

III. MORPHOLOGY

a. *Cothurnocystis elizae* Bather 1913

SYSTEMATIC POSITION: Phylum Chordata: Subphylum Calcichordata: Class Stylophora (Gill & Caster 1960). Order Cornuta (Jaekel 1900). Family: Cothurnocystidae Bather 1913. Genus: *Cothurnocystis* (Bather 1913). Type species.

OCCURRENCE: Only known from the hard, greenish siltstone of the Starfish Bed [Upper Ordovician, Ashgill Series, Drummuck Group]. All the material examined was from Thraive Glen, Girvan, Ayrshire, Scotland—the type locality. The associated fauna indicates a shallow water, marine environment.

MATERIAL: About 190 specimens collected by the Gray family and preserved in the British Museum (Natural History). The specimens are mostly still articulated as if suddenly buried. The plates have not been distorted by compaction of the

rock. The registration numbers are as follows: E 23130-1, E 23133-7, E 23139-41, E 23143-50, E 23152-9, E 23161-4, E 23166-7, E 23169-72, E 23174-86, E 23188-93, E 23201, E 23318, E 23329, E 23337, E 23342, E 23352, E 23394-6, E 23702-5, E 23713, E 23716-7, E 23719-27, E 23729, E 23731-7, E 23740-3, E 23745, E 23747, E 23749, E 23752-3, E 23757, E 23761, E 23766, E 28417, E 28420, E 28571-3, E 28575, E 28590-1, E 28603-8, E 28631-2, E 28635-46, E 28651, E 28654, E 28656-60, E 28663-4, E 28666-7, E 28884.

GENERAL SHAPE AND PLATE NOMENCLATURE: (Fig. 1a-g).

The animal consists of a theca and a stem. The theca is boot-shaped and, following Bather, an "ankle" and a "foot" part can be distinguished. The thecal skeleton consists of stout marginal plates to which are attached upper dorsal and lower ventral flexible integuments ("obverse" and "reverse" Bather 1913). The recognition of upper and lower surfaces of the theca is virtually certain, for all the thecal openings are on the dorsal side, and all the spikes for anchoring the theca to the bottom are ventral. Three prominent spines project from the anterior face of the theca and can be called the right oral appendage, left oral appendage and left appendage (tag, tongue and toespine of Bather 1913: 399; digital, glossal and spinal of Ubaghs 1963).

The marginal plates are numbered to right and left starting anterior to the stem and finishing at the mouth, the complete assemblage being as follows:

			Ubaghs 1963. Based on plate notation of Jaekel 1900
Notation	Name	Bather 1913	
M _{1LD}	first left dorsal marginal	Not shown	Not shown
M _{1LV}	first left ventral marginal	5	M ₁
M _{2L}	second left marginal	6	M ₂
M _{3L}	third left marginal	7	M ₃
M _{4L}	fourth left marginal (incl. left appendage)	8 (incl. toe spine)	M ₄ (incl. spinal)
M _{5L}	fifth left marginal	9 and 10	M ₅ and M ₆
loop	left oral appendage	tongue	glossal
M _{6L}	sixth left marginal	11	M ₇
M _{1RD}	first right dorsal marginal	Not shown	Not shown
M _{1RV}	first right ventral marginal	4	M _{1'}
M _{2R}	second right marginal	3	M _{2'}
M _{3R}	third right marginal	2	M _{3'}
M _{4R}	fourth right marginal	1	M _{4'}
roap	right oral appendage	tag	digital
M _{5R}	fifth right marginal	12	M _{5'}

A strut on the ventral surface connects M_{1R} and M_{5L}. Distinct spikes (S) are present on the ventral surfaces of M_{2R} (S_R), M_{2L} (S_{1L}), and M_{3L} (S_{2L}). Sutures are indicated M_{1LD/V}, M_{2/3R} etc.

The stem consists of three distinct parts: anterior, medial and posterior. The nomenclature used will be discussed later (p. 259ff).

THECAL OPENINGS: The openings of the theca are anatomically crucial and have caused much argument.

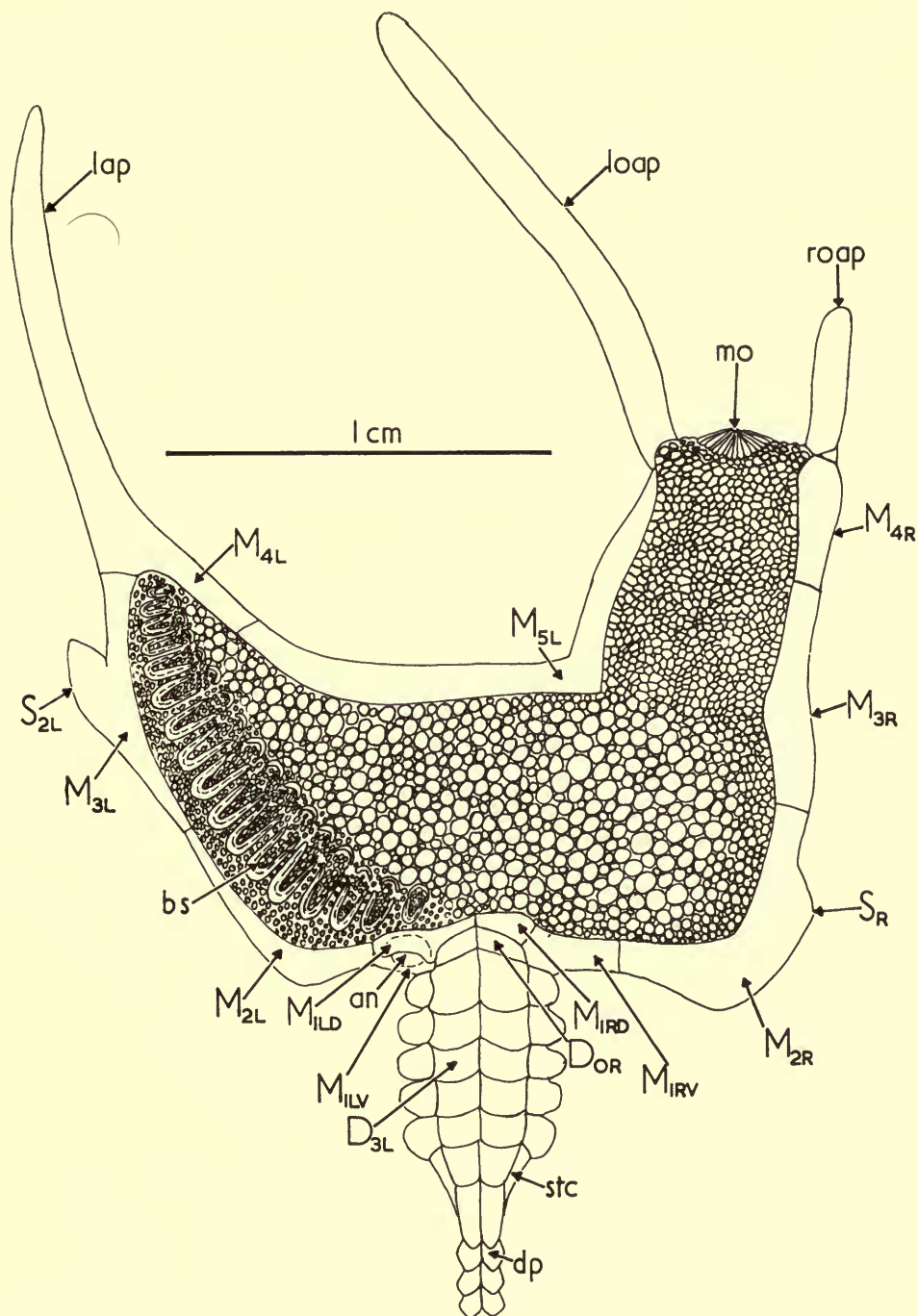


FIG. 1. *Cothurnocystis elizae*. Reconstruction of external features. a. dorsal ; b. ventral aspect ; c. stem from left ; d. theca from left ; e. "ankle" region from left ; f. theca from right ; g. posterior aspect. an = anus ; dp = dorsal plate of posterior stem ; lap = left appendage ; loop = left oral appendage ; roap = right oral appendage ; stc = stylocone ; str = strut ; vo = ventral ossicle without boss ; vob = ventral ossicle with boss.

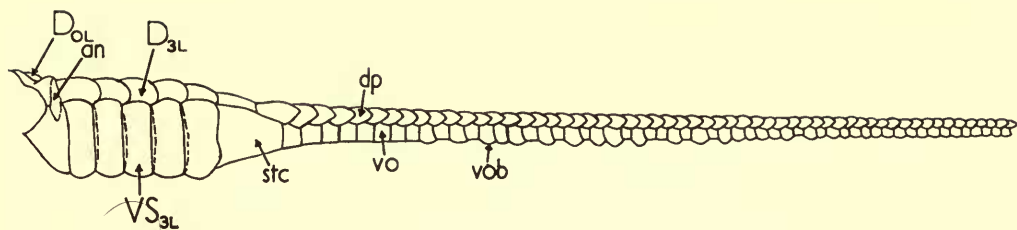


FIG. 1c.

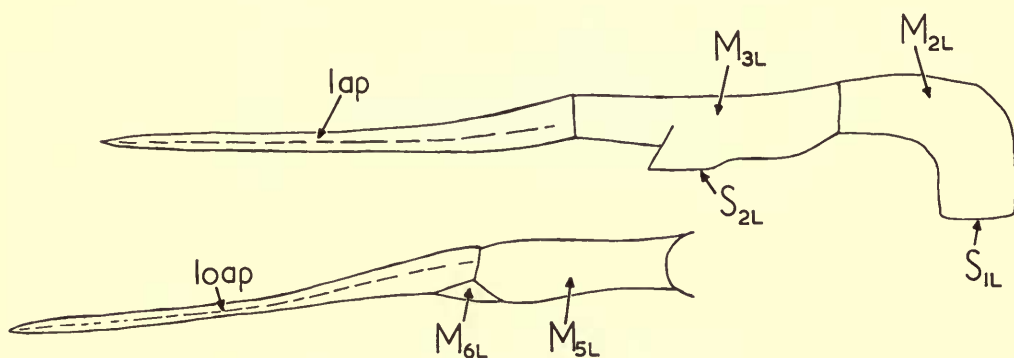


FIG. 1d, e.

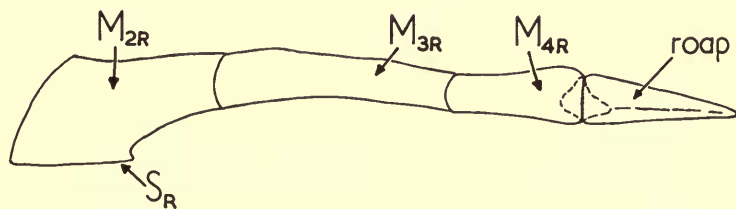


FIG. 1f.

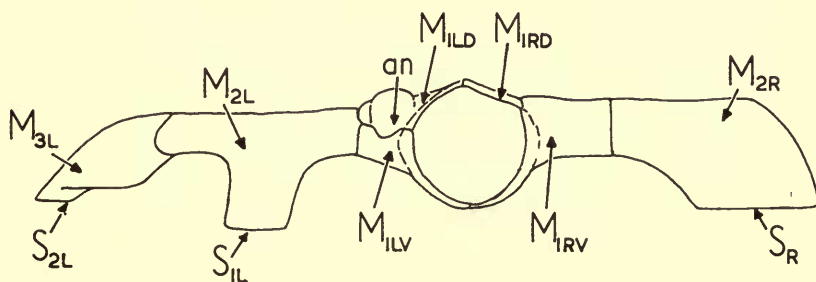


FIG. 1g.

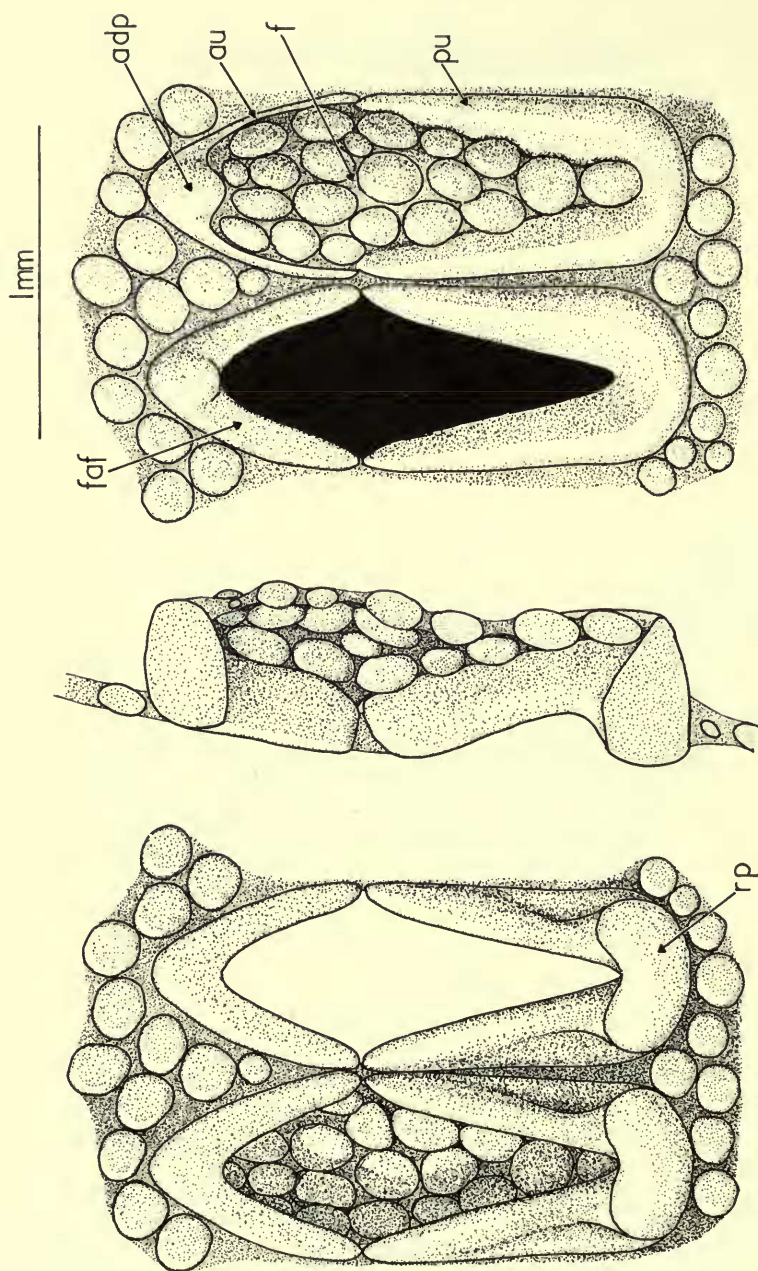


FIG. 2. *C. elizae*. Structure of branchial slits. a. internal aspect ; b. longitudinal section ; c. external aspect. adp = antero-dorsal process ; au = anterior u-plate ; f = flap ; fap = flap attachment facet ; pu = posterior u-plate ; rp = reniform process.

There were, first, about 16 elliptical openings (bs) in the left, posterior part of the dorsal integument. Their detailed structure (Fig. 2 a-c; Pl. 1, figs. 1, 7, 8) can best be studied with latex casts. Each opening is surrounded by a frame consisting of a smaller anterior u-shaped plate (au) and a larger posterior one (pu) with an articulation between them. The anterior dorsal part of the anterior u-plate bears an antero-dorsal process (adp), of very variable size. Posterior to this process a flap (f) is attached by flap attachment facets (faf). This flap is convex outwards and concave inwards and contains many small plates which are often bigger towards the margins than in the middle of the flap. The flap must have been flexible in life and the edges of its free, posterior part were able to rest on the posterior u-plate, so as to shut the opening completely. There is no doubt that the flap was attached to the anterior u-plate rather than the posterior one since, when these two plates were displaced relative to each other after death, the flap was sometimes displaced to one side of the posterior u-plate (flaps f in Pl. 1, fig. 8) but remained connected to the anterior u-plate in the normal way. The posterior, internal end of the posterior u-plate was produced into a flat-topped reniform process (rp in Fig. 2a; Pl. 1, fig. 1).

Bather's descriptions of these openings (1913 : 404, fig. 16) is very different from the above except as regards the two u-plates of the frame. In his view the small plates inside each slit were biserial "cover plates" attached to the edges of the posterior u-plate. This interpretation may have been suggested by the fact that the plates round the edge of each flap tend to be larger than those in the middle. Using latex casts, however, which were not of course available to Bather, the attachment of the flap to the anterior rather than the posterior u-plate can easily be demonstrated.

The structure of these openings strongly suggests outlet valves. When the water pressure beneath the branchial slits increased, the flaps would lift from the posterior u-plates. This would happen partly because of the flexibility of the flaps, and partly because the frames of the slits would bend upwards at the articulations between anterior and posterior u-plates, to follow the bulging of the integument. When the flaps opened water would escape. As the water pressure beneath the openings consequently decreased, the flaps would close and prevent water from entering. The outwardly convex, arcuate section of each flap, maintained by the u-shape of the anterior u-plate and by a slight stiffness imparted by the little plates of the flap, is admirably suited to resist pressure from outside and confirms the outlet valve interpretation. This interpretation is also supported by the presence of a differently constructed outlet-valve system in a corresponding position in *C. curvata* (p. 266). The slits of both species do not resemble inlet structures and Bather's view that they were mouths, resting as it does on the interpretation of the flap plates as biserial cover plates, is without foundation. It is unlikely that the slits were gonadial (*pace* Jaekel 1918 : 122) or excretory since a much less elaborate structure would, in these cases, suffice. By far the most probable interpretation is that they were exhalant and homologous with branchial slits, as Gislén suggested (1930 : 213).

Another opening, not mentioned in the literature (an in Figs. 1a, g, Fig. 3a, d ;

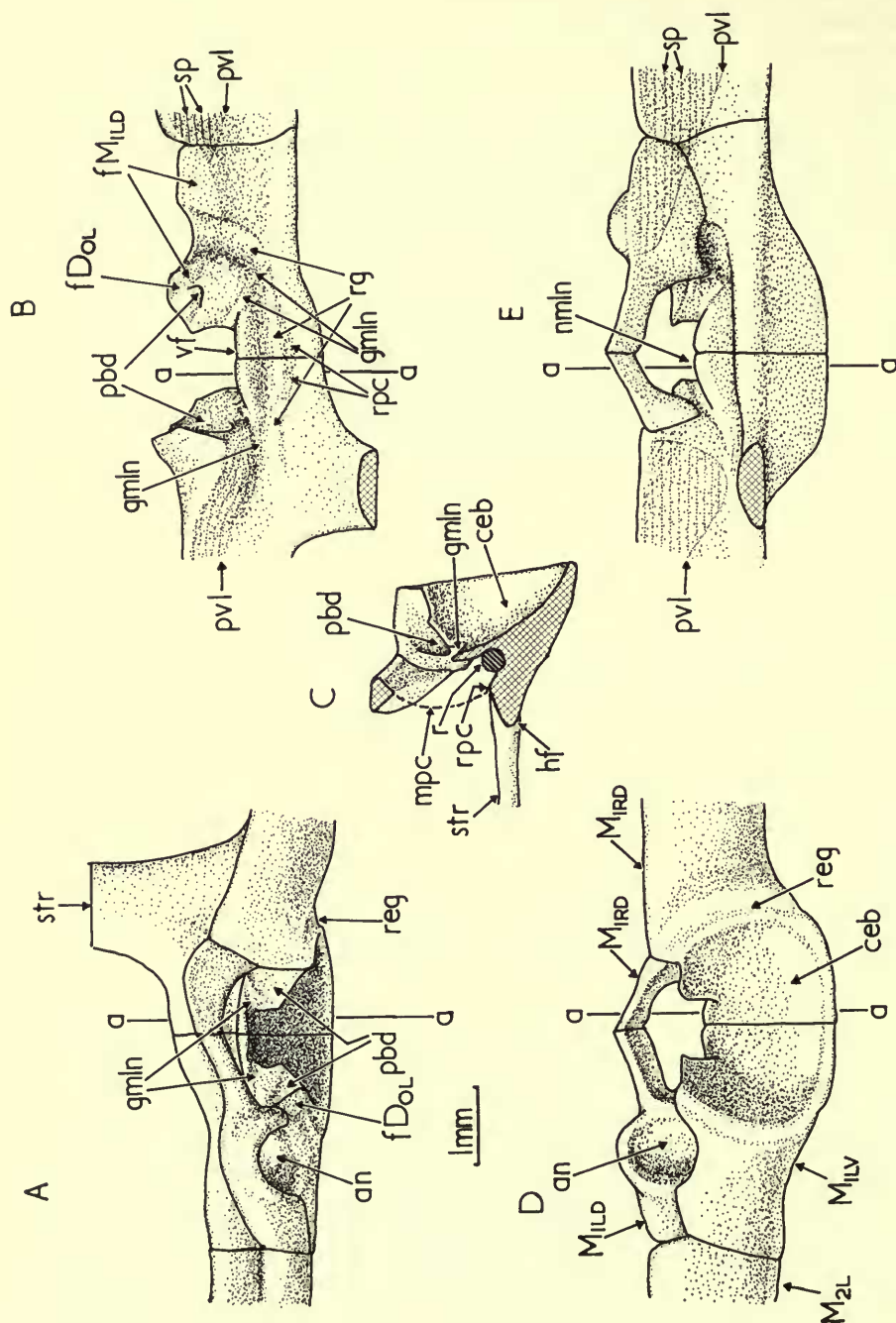


FIG. 3. *C. elizae*. Structure of region just anterior to stem. A. dorsal; B. anterodorsal aspects; C. longitudinal section through a-a; D. posterior; E. anterior aspects. an = anus; ceb = cerebral basin; fDoL = facet for DoL; fM1LD = facet for M1LD; gmln = groove for median line nerve; hf = horizontal flange of M1R and LV; mpc = membrane limiting posterior coelom anteriorly; nmln = notch for median line nerves; pbd = depressions for pyriform bodies; r = rectum; reg = reception groove for anterior stem; rg = rectal groove; rpc = ridge limiting posterior coelom anteriorly; sp = striations of pharynx; vf = vertical flange of M1L and RV; str = strut.

Pl. 1, figs. 2, 10) whose function was clearly different from that of the gill slits, lies just posterior to the most median of these, to the left of the stem, on the suture M_{1LV}/M_{1LD} . It connects with a groove (rg) which first goes down vertically between M_{1LV} and M_{1LD} and then turns to the right and runs over the dorsal surface of the horizontal flange of M_{1LV} and M_{1RV} (hf in Fig. 3c; Pl. 2, fig. 8). This groove could well represent the course of the rectum, in which case the opening connected to it would be the anus. Such an interpretation is confirmed by the position of the opening, for the streams of water from the most median gill slits, flowing backwards parallel to the flaps, would serve to wash faeces away from the anus. The opening is, incidentally, far too large to have been a hydropore.

The only other thecal opening (mo in Fig. 1a; Pl. 2, fig. 4) lies at the anterior end, between the right and left oral appendages. The pointed plates round this opening give it the appearance of an anal pyramid, as Bather asserted (1913 : 412). However, there is no compelling reason why such a structure must have served as an outlet, and indeed, if the other openings represent gill slits and anus, then this last opening can only be the mouth, as Gislén suggested (1930 : 213). This agrees with the fact that it is much the largest opening in the theca.

An interesting peculiarity of preservation supports the present interpretation of the thecal openings. As already stated the specimens studied seem to have died by sudden burial. It is sometimes found (specimens E 23148, E 23150, E 28641) that the integuments of the theca to the right, but not to the left, of the strut are separated by a layer of rock. This is presumably because the fall of mud that killed the animal, entered the mouth before this had time to close and filled up the right-hand side of the theca. On the other hand, only a very small amount of mud could enter through the gill slits, whose flaps would shut when mud was piled on top of them.

THE CHAMBERS OF THE THECA: The features of the internal cast, integuments and external shape of *C. elizae* indicate that the theca was divided into four chambers (Fig. 4).

The existence of the first of these chambers, filling the "ankle" part of the theca, is shown by:—(a) The constant presence of a low ridge running dorso-ventrally on the inside of M_{3R} , just opposite the sharp angle in M_{5L} which separates "ankle" from "foot" (rbcr in Pl. 1, fig. 7; Pl. 2, figs. 1, 3; Pl. 3, fig. 1). (b) The presence in two specimens (rbcl in Pl. 3, fig. 1, and E 23725) of a corresponding, parallel ridge on the inside of M_{5L} . In these specimens this ridge is obviously distinct from the sharp angle just referred to, though in other specimens it is presumably inseparable. (c) The plating of the dorsal integument of the "ankle" is different from that of the "foot" (see below, p. 258). (d) The gross separation between ankle and foot visible externally. This first chamber, here called the buccal cavity, is probably homologous with the buccal cavity of chordates and the vestibule of crinoids.

Considering now the "foot" part of the theca, an undulating line can often be seen on the internal mould separating an upper from a lower part (pvl in Fig. 3b, e; Pl. 1, fig. 9; Pl. 2, figs. 2, 5). Followed from left to right (Fig. 4) the line rises from the ventral margin at point o/1 on M_{3L} , reaches a peak at point 1, on the

suture $M_{2/3L}$, descends to near the ventral border again at point $1/2$ in the middle of M_{2L} , and rises to the dorsal margin of the frame at point 2, on M_{1LD} , just to the right both of the anus and of the most median gill slit. It leaves the dorsal margin at point 3, on M_{1RV} and descends vertically to point $3/4$, which is just above the ventral border of the marginal frame. It then rises to point 4, near the suture M_{1RV}/M_{2R} , falls to point $4/5$, situated at the "heel" in the middle of M_{2R} , and

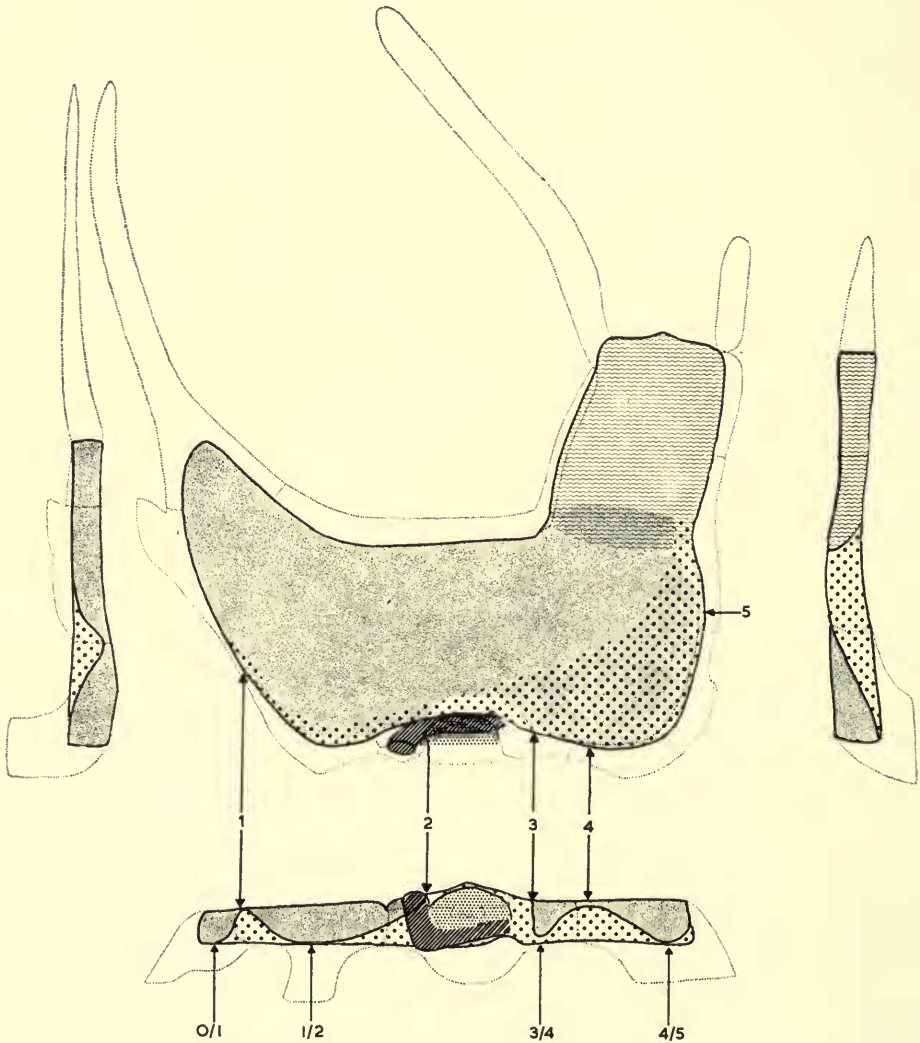


FIG. 4. *Cothurnocystis elizae*. Chambers of the theca. a. left ; b. dorsal ; c. right ; d. posterior aspects. $0/1$, $1/2$, $3/4$, $4/5$ = points where pharyngo-visceral line nears or reaches the ventral side of theca. 1, 2, 3, 4, 5 = points where pharyngo-visceral line nears or reaches dorsal side of theca. Stipple used as in Text-fig. 14.

then rises to point 5 on M_{3R} , some distance behind the posterior border of the buccal cavity. In very large specimens (Pl. 2, figs. 2, 5; Fig. 3) the area of the theca internal mould above this undulating line is horizontally striated (sp). There is no trace of the lower chamber on the inside of the frame along the anterior margin of the "foot" part of the theca.

This undulating line gives the strong impression of separating two chambers and the striae above it confirm that the area dorsal to it corresponded to one and the same chamber. This upper chamber must have opened by the gill slits as is confirmed by the fact that, on the front surface of M_{ILD} , its distribution coincides with the presence of slits in the dorsal integument. The upper chamber must therefore have been the pharynx and, if so, the lower chamber would be the main visceral cavity, henceforward called the anterior coelom. The main mass of the viscera would have lain on the ventral integument somewhat to the right of, and anterior to, the stem. It is from this general region that the rectal groove emerges. The separate existence of buccal cavity and pharynx is supported by hydrodynamic considerations and by peculiarities in the plating of the integuments (see below, p. 258). The undulating line will henceforward be termed the pharyngo-visceral line.

The peaks in the pharyngo-visceral line at points 1 and 4, which are near the sutures $M_{2/3L}$ and $M_{1RV/2R}$, may be due to the optic nerves ascending almost to the dorsal side at these points, for the optic nerves of *Mitrocystites mitra* break through on to the dorsal surface at corresponding positions. This implies that at their first appearance in the cornutes the optic nerves were totally internal and came into existence before the eyes, in accordance with Studnička's theory (Walls 1942 : 126). Totally internal optic nerves would have been quite capable of functioning as light sensors. The gradual ascent of the pharyngo-visceral line between points 4/5 and 5 reflects the fact that pharynx and buccal cavity had to be connected, for obvious reasons, so that the anterior coelom in this region was pushed over to the right.

The last chamber (posterior coelom in Fig. 4; pco in Pl. 1, fig. 9; Pl. 2, fig. 1) lay just anterior to the stem and was largely bounded by skeleton. Anteriorly it seems to have had a roughly hemispherical limiting membrane (mpc in Fig. 3c) which touched the skeleton (i) at the posterior surface of M_{ILD} and M_{IRD} , and (ii) on the dorsal surface of the horizontal flanges (hf) of M_{ILV} and M_{1RV} , in the shallow, curved depression limited anteriorly by the ridge rpc (Fig. 3B, C.). The rectum (r in Fig. 3C), whose course is indicated by the rectal groove (rg), ran beneath this chamber, from right to left, and was presumably coated dorsally by the limiting membrane of the chamber. The posterior limit of the chamber would correspond more dorsally to the front of the brain. More ventrally it would correspond to the front of the vertical flanges (vf) of M_{ILV} and M_{1RV} . The posterior coelom is probably homologous to the aboral coelom of echinoderms.

To sum up, therefore, the four chambers recognizable in the theca of *C. elizae* were the buccal cavity, pharynx, anterior coelom and posterior coelom. The same chambers can be demonstrated, with variations and additions, in the other forms studied.

THE INTEGUMENTS AND MODE OF FEEDING: In very young specimens all the plates of the integuments were almost uniformly polygonal with rounded corners. In middle-sized individuals, however, there was considerable differentiation (Fig. 1a, b; Pl. 1, fig. 7; Pl. 2, fig. 3). As regards the dorsal integument, in the "ankle" region it contained polygonal plates while in most of the "foot" it contained large, circular or spheroidal plates. In the gill slit region it contained very small, rounded plates and must have been very thin. The ventral integument in middle-sized individuals contained (Fig. 1b; Pl. 2, fig. 3) polygonal plates except in a crescentic region near the anterior side of the "foot" (acp in Pl. 2, fig. 3), mainly left of the strut, where the plates were circular. In all cases circular plates touched their neighbours, if at all, at only five or six points, whereas polygonal plates touched their neighbours all round their edges. The integuments of large individuals (Pl. 1, fig. 10; Pl. 2, fig. 1) were like those of middle-sized ones except that the plates of the whole of the dorsal integument, save the small plates of the gill slit region, were large and circular. In the "foot" region, however, the plates of this integument were separated by larger spaces than those of the ankle region, which is comparable to the condition in middle-sized specimens.

The functional significance of the different sorts of integumental plates is related to the underlying thecal chambers. Wherever the pharynx touched the integuments, except in the gill-slit region, the plates tend to have larger interspaces than elsewhere. This applies both to the dorsal integument over most of the "foot" region and to the left, anterior part of the ventral integument. Such interspaces could well have contained muscles, and the corresponding parts of the integument would have been involved in pumping. The thin, small-plated integument of the gill-slit region would have been very flexible, which would clearly have made the region more efficient as a valve. The integument of the buccal cavity and the parts of the ventral integument on which the anterior coelom rested would not have been so directly involved in pumping as the parts touching the pharynx, and were consequently less well muscled.

If the pharynx was the main pumping region it would be hydrodynamically advantageous to have a valve just upstream of it, at its anterior end, to prevent forward flow. This valve, between pharynx and buccal cavity, would be the velar valve. Water may have entered the pharynx from the buccal cavity by muscular outward flexing of the pharyngeal regions of the integuments or through being driven in by cilia lining the buccal cavity and pharynx. Expulsion of water from the pharynx must have been by contraction of the muscles of the pharyngeal walls. Such contraction would tend to pull the frame inwards and to cause collapse at the middle of the anterior part of the frame, which is convex inwards. The strut in the plane of the ventral integument is perfectly placed to prevent such collapse. Phylogenetically speaking, this strut is a remnant of the completely rigid ventral shield of the Upper Cambrian *Cothurnocystis americana* Ubachs 1963, in which there was a dorsal integument, and of the ventral skeleton of the Middle Cambrian *Ceratocystis perneri* Jaekel, where the whole theca was rigid.

C. elizae must have been a "deposit feeder", in Hunt's terminology (1925 : 567), grazing on "the detritus deposited on the bottom and associated micro-organisms."

This is apparent since the mouth was about level with the sea bottom and since the inhalent current could only have been horizontal. The right oral appendage has sharp edges, an almost flat lower surface and a convex upper surface, and is articulated by a vertical ridge on its base to a corresponding ridge on M_{4R} (Pl. 2, fig. 4). The articulation is flanked by spaces that could well have contained muscles. This appendage seems to be adapted for waving from side to side, scraping and churning-up the surface layer of the sea bottom. The resulting suspension would be sucked in through the mouth. It is advantageous to a deposit feeder to move over the surface, grazing the bottom as *C. elizae* was probably able to do (p. 265). By contrast, *C. curvata* was probably a suspension feeder, which explains the coexistence of the two types as well as many points of difference (p. 271). In both species food particles would presumably have been carried into an oesophagus by mucus streams on the internal surface of the pharynx.

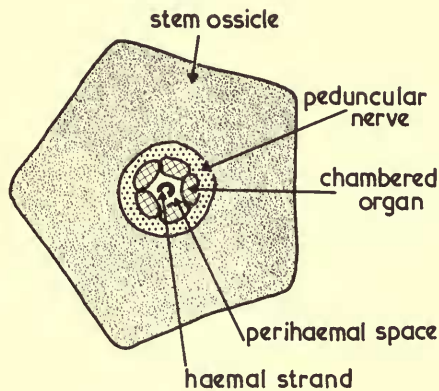


FIG. 5. Transverse section of the stem of a crinoid, based on Reichensperger (1905).

A curious feature of some young specimens is a number of specially large plates (crestal plates, cp in Pl. 1, fig. 2) in the dorsal integument. These correspond in position to a clearly marked line of plates in *Cothurnocystis americana* (Ubaghs 1963) and to the carinae on the dorsal surface of *Ceratocystis perneri*. In *C. elizae* their appearance is only sporadic and they were probably non-functional.

THE STEM: The nearest living analogue to the stem of a stylophoran is the stem of a crinoid. The probably ancestors of crinoids were the eocrinoids which include forms with distinct stems from the Middle Cambrian (*Gogia* Walcott, see Robison 1965). These are roughly contemporary with the first cornute so that, in view of the obvious gaps in the record, there is no chronological reason why the stems of crinoids and Stylophora should not be homologous.

The stem of a crinoid will now be compared with the tail of a fish. The best anatomical account of a stalked crinoid is that of Reichensperger (1905) (see Fig. 5). The central lumen of the stem contains, on the outside, the peduncular nerve, with the fibres running longitudinally. Inside this is the chambered organ, a turgid structure consisting of five adjacent tubes. Inside this is a space (here called the

perihæmal space) in which lies a narrow tube called the hæmal strand. The top of the chambered organ is at the proximal end of the stem. Here the five constituent tubes swell slightly and bend inwards to touch the hæmal strand, so separating the perihæmal space of the stem from the thecal cavity. The hæmal strand continues out of the stem into the theca, where it joins the axial organ. The hæmal strand presumably functions as a blood vessel, since otherwise it is difficult to see how nutrients could reach the stem. Round the top of the chambered organ is situated the aboral nerve centre, which is the meeting-place of the aboral nerves of the theca with the peduncular nerve. The chambered organ presumably functions as the hydrostatic skeleton of the stem, helping to hold the ossicles in alignment. It is of mesodermal origin, arising as five pouches of the aboral coelom (Seeliger 1892). The origin of the aboral nervous system has never been seen, but it appears to arise later than the chambered organ.

Though never reported, muscles must exist in a crinoid stem which, in larval *Antedon*, can be bent at will (Chadwick 1907 : 37; Dimelow 1959 : 21). Hyman (1955 : 60) has pointed out that some of the "elastic" fibres in the cirri must be muscular, since these organs also can be bent at will. Elastic fibres have been reported in the stem itself, and if some of these are muscular then the nerves going from the peduncular nerves to the stem ossicles, which so puzzled Reichensperger (1905 : 30), could be their nerve supply.

The resemblances of a crinoid stem to a fish's tail are very striking. The chambered organ is like the notochord in structure, presumably in function, and to a lesser extent in origin. The peduncular nerve can be compared with the dorsal nerve cord, being applied to the surface of the chambered organ as the dorsal nerve cord is applied to the notochord. The aboral nerve centre is like the brain, for it lies at the "anterior" end of the chambered organ (= notochord) and peduncular nerve (= dorsal nerve cord) and sends out aboral (= cranial) nerves into the theca. The muscles which must exist in the stem would correspond broadly to those of the tail. The hæmal strand and perihæmal space could correspond broadly to caudal artery and veins.

Furthermore the aboral nerve centre is physiologically the brain of a crinoid. Thus Langeloh (1937 : 272) showed that if it is excised the animal becomes limp and fails to carry out complicated patterns of behaviour which are otherwise instantaneous. If, however, an electric current is applied to the site of the excised centre, the appropriate reaction follows at once. The centre functions not so much in co-ordination as in summation of stimuli. In this it resembles the brain of a fish (Gray 1936; Gray & Sand 1936*a, b*).

A crinoid stem certainly differs from a fish's tail in a number of ways. It is pentamerous, with the homologue of the notochord divided into five parts and completely surrounded by the homologue of the dorsal nerve cord. Also the stem has a calcite skeleton, has the hæmal strand inside the chambered organ and is attached distally. The stylophoran stem was intermediate, for it certainly had a calcite skeleton, probably had a "hæmal strand" or peduncular vessel inside the notochord, and may have been attached distally when very young. On the other hand it lacked all sign of pentamery, in common with the theca, and, at least in mitrates,

had the dorsal nerve cord exclusively dorsal to the notochord. Also the segmentation of a fish's tail almost certainly corresponds with that of a stylophoran stem as regards the soft parts, but probably not with that of a crinoid stem. The correspondence of a crinoid or stylophoran stem with a fish's tail agrees with Marcus's statement (1958 : 50) that " the metamerism of the chordate trunk is fundamentally a subdivision or multiplication of the metacoel ".

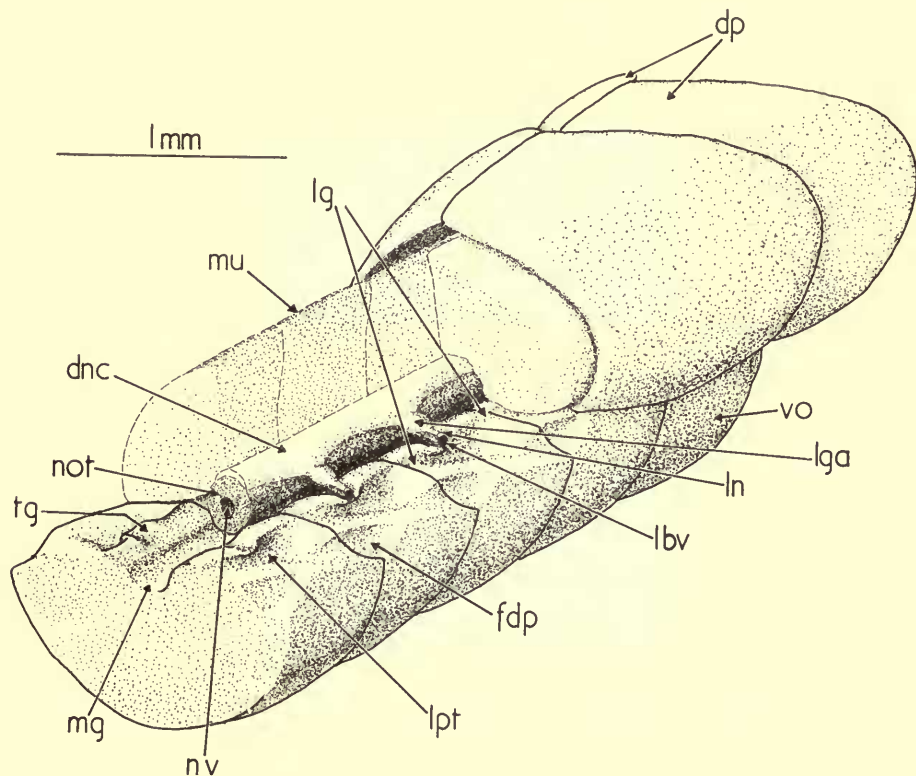


FIG. 6. *C. elizae*. Block diagram of portion of posterior stem. dnc = dorsal nerve cord; dp = dorsal plate; fdp = facet for dorsal plate; lbv = lateral blood vessel; lg = lateral groove; lga = lateral ganglion; ln = lateral nerve; lpt = lateral pit; mg = median groove; mu = muscle; not = notochord; nv = notochordal vessel; vo = ventral ossicle; tg = transverse groove.

The stem of *C. elizae* will now be described, beginning at the posterior end where the skeleton is most complicated and informative.

The posterior stem (Fig. 1, 6; Pl. 1, figs. 4, 5, 7; Pl. 2, fig. 9; Pl. 3, figs. 2, 3) consists of about 60 segments and ends abruptly. Each stem has a solid, hemicylindrical ventral ossicle (vo) and a dorsal arch formed of paired dorsal plates (dp) which meet mid-dorsally at a suture. Each dorsal arch imbricates over the front of the one behind it. Near the middle part of the posterior stem some of the ossicles project ventrally in a boss (Fig. 1c; Pl. 1, fig. 4) and the posterior faces of such ossicles

are not plane, but curved about a horizontal axis. Such cylindrical surfaces would make it easier to bend the column of ventral plates vertically (Fig. 7) and it follows that the middle part of the posterior stem was vertically more flexible than the more anterior part. Towards the posterior end of the stem, the ventral bosses coalesce to form a blunt ventral keel.

The dorsal surface of each ventral ossicle is complicated (Fig. 6; Pl. 2, fig. 9). There is a median groove (mg) which runs the length of the posterior stem and connects anteriorly with the lumen of the stylocone. On each side of this groove

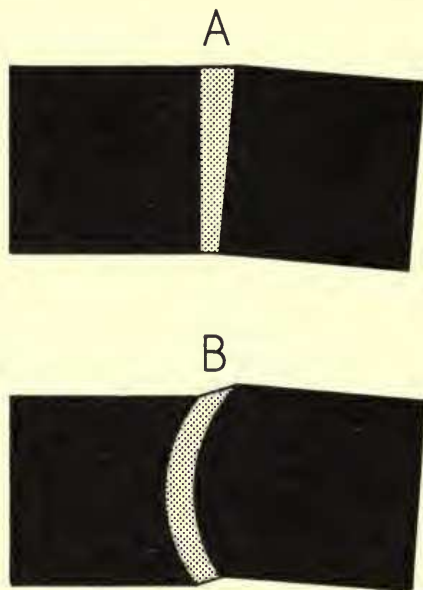


FIG. 7. A. Plane, and B. cylindrical interossicular joints. Bending at a plane joint involves compression or dilatation, or both, of the interossicular soft tissue. Bending at a cylindrical joint can occur by torsion of the soft tissue.

are lateral grooves (lg) which on each ossicle are deepened into lateral pits (lpt). Outside the lateral grooves are facets for the reception of the dorsal plates (fdp). Paired transverse grooves (tg) connect the lateral pits with the median groove.

The median groove of *C. elizae* probably contained the chambered organ or notochord, coated, at least partially, with the peduncular nerve or dorsal nerve cord. By analogy with the mitrates the nerve was perhaps restricted to the dorsal surface as shown in Fig. 6. The imbricate dorsal plates show that the posterior stem could flex upwards. For this, muscles (mu) would be needed. They would lie in the space between dorsal plates and ventral ossicles and would be seated in the lateral grooves. They were probably divided into muscle blocks, the divisions between which, by analogy with *C. curvata* and the mitrates, would correspond to the transverse grooves. Muscles would need nerve and blood supply. The transverse grooves may possibly mark the course of lateral blood vessels connected with

a central peduncular blood vessel (nv in Fig. 6) in the notochord that was homologous with the haemal strand of crinoids. Along the dorsal surface of the lateral blood vessels, by analogy with the mitrates, lateral nerves may have run. The extensor force opposing the muscles was probably due to the column of ventral plates which may have been elastic like a recent crinoid stem when wet (personal observation). The abrupt end of the posterior stem is of some interest. It strongly suggests that at some stage in the life history the stem extended posterior to what now remains. Indeed, it is possible that when very young the animal was attached by a holdfast, like a crinoid, from which it later broke free. An abrupt end to the stem is also found in all the other forms studied.

Ubaghs (1961*b*) has interpreted the structures of the posterior stem of both cornutes and mitrates as representing a water vascular system (median groove = main water vessel; lateral grooves = lateral water vessel; lateral pits = sites of tube feet; dorsal plates = cover plates; stem as a whole = arm of asterozoan). This seems quite unacceptable for reasons which will be set out in detail after the mitrates have been discussed.

The medial stem (Fig. 1; Pl. 1, figs. 3, 4, 7) corresponds to two segments and is made up of the stylocone (stc) ventrally and two pairs of plates dorsally. The large anterior cavity of the stylocone connects with the median groove of the posterior stem and is flanked by two pairs of lateral pits, with transverse grooves leading to them. The stylocone resembles two fused ventral posterior stem ossicles, with which it is serially homologous. It is also presumably homologous with the paired ventral plates of the anterior stem. It served as a rigid barrier to separate the powerful muscles of the anterior stem, which moved the stem sideways, from the muscles and ventral ossicular column of the posterior stem, which moved it up and down. If the muscle blocks of the posterior stem and anterior stem had formed continuous columns, separated only by myocommata, then contractions of the anterior muscles would have produced functionally irrelevant elongations of the more anterior muscle blocks of the posterior stem on one side only.

The anterior stem is offset downwards from the theca (Fig. 1*b*, *c*), so that its median ventral line is lower than the ventral surface of the latter. It consists of five rings of plates (cf. Ubaghs 1961*a*; Caster 1952) enclosing a large lumen. Each ring has four plates—left, dorsal and ventral and right, dorsal and ventral—denoted by D_{nL} , VS_{nL} and D_{nR} and VS_{nR} in ring n . The dorsal plates are much smaller than the ventral plates. Each one is apposed to its antimere at the median line and imbricates below the corresponding ventral plate ventrally. The dorsal plates are evidently serial homologues of those of the medial and posterior stem.

The ventral plates of the anterior stem are crescentic in anterior or posterior aspect. They are therefore thinner near their dorsal and ventral ends than near the middle. The posterior surface is always almost plane. The anterior surface is either almost plane or produced into an admedian imbrication flap (if in Pl. 1, fig. 10) which is not developed near dorsal and ventral ends of the plate.

The length of a ventral plate, measured along the length of the stem and omitting the imbrication flap, is greater near the mid-line than more laterally (Pl. 1, fig. 10). Successive pairs of ventral plates touched each other ventrally, without imbrication,

and almost touched dorsally. There would therefore, when the anterior stem was held straight, have been gaps between successive plates at right and left, and these would have allowed lateral flexing.

The first pair of ventral plates (VS_{1L} , VS_{1R}) fitted into a reception groove in M_{1RV} and M_{1LV} (reg in Fig. 3d). The gap between the corresponding dorsal plates (D_{1L} , D_{1R}) and the arch formed by M_{1LD} and M_{1RD} was filled by a pair of dorsal plates (D_{0L} and D_{0R}) with no ventral plates corresponding.

The skeleton thus shows that the anterior stem was adapted to flex sideways but not up and down, and the way the specimens are preserved confirms this. The anterior stem is found flexed in any position from extreme right to extreme left as it lay at the moment of burial (e.g. Pl. 1, figs. 4-7). The soft parts of the anterior stem must have consisted mainly of powerful muscles, presumably divided into segmental blocks. An anti-compressional structure (notochord or chambered organ), which would have maintained the alignment of the skeletal rings, is likely to have existed. It would be a forward continuation of the notochord of the posterior and medial stem, would contain the peduncular blood vessel and would be coated by the peduncular nerve or dorsal nerve cord. Segmental nerves and blood vessels to the muscles must also have been present.

THE BRAIN: By analogy with a crinoid the aboral nerve centre or brain of *Cothurnocystis elizae* must have occupied a prominent basin (cerebral basin, ceb in Fig. 3) excavated in the postero-ventral faces of M_{1RV} and M_{1LV} where the stem joins the theca (Pl. 2, fig. 6).

A median notch (nmln) in the dorsal edge of plates M_{1RV} and M_{1LV} leads to two grooves (gmln), running outwards and downwards, on the anterior face of the vertical flange (vf) of these plates (Fig. 3, Pl. 2, fig. 8). The left groove can sometimes be followed to the floor of the rectal groove (Pl. 2, fig. 7). The right groove is somewhat shorter, probably because the structure that it carried left the skeleton earlier. To right and left of the median notch are two triangular depressions (pbd) excavated in the dorsal surface of M_{1RV} and M_{1LV} .

The soft structures indicated by the notch, grooves and depressions, since they came off the brain, were probably nervous. The depressions probably carried ganglia, corresponding to the pyriform bodies (pb in Figs. 19a, 27a) of mitrates. The grooves probably carried nerves (median line nerves). Since the left one passed under the rectum this, at least, was more ventral than any nerves of which there is evidence in mitrates, with the possible exception of the nerves n_0 . The optic nerves, whose possible terminations have been indicated above, presumably left the brain more dorsally, through the notch, and passed dorsal to the rectum.

ONTOGENY: Very small specimens much resemble adults. At a length (measured from the stem base to the anterior end of M_{5L}) of 6 mm., gill slits already existed and extended back to the anus, as in the adult. Their number could not be determined. The smallest specimens (e.g. Pl. 2, fig. 4) do not have the stem offset ventrally with respect to the theca and lack ventral spikes, which first appear on the sides of the marginals. The number of rings in the anterior stem is smaller (only 3 in Pl. 1, fig. 3) and the number of ossicles in the posterior stem is about

fifteen, as opposed to about 60 in the adult. The smallest specimens have the ventral mouth frame oblique to the "ankle" region, the left end being more anterior than the right.

POSTURE AND MOVEMENT: The bizarre shape of *C. elizae* calls for a reconstruction of its habits (cf. Bather 1913 : 415; 1928; Gislén 1930 : 217).

As Bather and Gislén said, the theca must have rested on the sea bottom, supported on the ventral processes and anterior appendages, and with the dorsal surface upwards. The right oral appendage was motile (see above, p. 259). Of the remaining fixed processes and appendages, four are roughly parallel to each other (the left-hand spikes S_{1L} and S_{2L} , and the left oral and left appendages), whilst the remaining one (the right-hand spike S_R) is perpendicular to the others, cf. Fig. 1b. In life the anterior appendages would have dipped down anteriorly into the mud. The spikes S_{1L} and S_{2L} (Pl. 1, fig. 6) have sharper points anteriorly than posteriorly. S_R is always flat-bottomed and S_{1L} sometimes so.

When at rest on the bottom the theca could not have moved anteriorly, for the appendages and left-hand processes would have been forced into the sea-floor. This is the more true since S_R , which ends ventrally in a flat suitable for resting on the sea-floor, and the anterior stem, which is distinctly offset ventrally, would have raised the posterior part of the theca. The theca appears to be adapted to slip posteriorly in a direction parallel to the two fixed appendages (lap and loop) and the two left-hand spikes (S_{1L} and S_{2L}), and perpendicular to the right-hand spike (S_R). The obvious motility of the stem supports Gislén's suggestion (1930 : 217) that it was the main organ of movement. It is suggested here that it acted by pulling the theca *backwards* across the sea floor in the direction indicated above. The sea floor would be gripped by the ventral bosses on the posterior stem and by bending the tip downwards. The power stroke would be applied by flexing the anterior stem to left or right as appropriate.

Such a mode of operation explains: 1. the specialization of the parts of the stem for different planes of flexion; 2. the exact forms of the spikes and fixed appendages of the theca, which would serve admirably to prevent yawing and also to prevent forward movement during the return stroke of the stem; 3. the concentration of ventral bosses for gripping the sea-floor, and curved interossicular surfaces for downward flexion in the middle and posterior parts of the posterior stem.

Many features show that, when resting on the sea-floor, the usual direction of movement of the other forms studied was also backwards.

b. *Cothurnocystis curvata* Bather 1913

SYSTEMATIC POSITION: See *C. elizae*. Both species belong to the Family Cothurnocystidae. Professors Caster and Ubahgs are about to create a new genus for *C. curvata* (personal communication). This is certainly justified.

OCCURRENCE: As *C. elizae*.

MATERIAL: About 40 specimens, collected by the Gray family and preserved in the British Museum (Natural History). The registration numbers are as follows: E 23128, E 23132, E 23142, E 23151, E 23160, E 23165, E 23168, E 23173, E 23701,

E 23715, E 23728, E 23738, E 23739, E 23744, E 23748, E 23750-1, E 23754, E 23756, E 23758, E 23767, E 28427, E 28551, E 28552, E 28555, E 28574, E 28609, E 28617, E 28630, E 28633-4, E 28647-50, E 28652-3, E 28655, E 28661-2, E 28665. Also G.S.M. 60839 from the Geological Survey & Museum, London and 1958.1.252 from the Royal Scottish Museum, Edinburgh.

GENERAL SHAPE AND PLATE NOMENCLATURE: The general shape of the theca (Fig. 8a-e) is much like *C. elizae* but more symmetrical. The most obvious difference is the presence of only one oral appendage—a fixed structure probably corresponding to the left oral appendage of *C. elizae*. In addition the anterior part of the theca is convex upwards, whence the specific name. The marginal plates are numbered according to the scheme used in *C. elizae*, but homologous plates do not always bear the same numbers, as the table below shows.

C. curvata

Bather 1913	Present notation	Homologous plate in <i>C. elizae</i>
Not shown	M _{1LD}	M _{1LD}
5	M _{1LV}	M _{1LV}
6 and 7	M _{2L}	M _{2L}
	—	M _{3L}
8	M _{3L} left appendage	M _{4L} left appendage
	M _{4L}	—
9, 10 and 11	M _{5L} anterior strut plate	M _{5L} anterior strut plate
Not shown	right appendage	left oral appendage
	—	M _{6L}
Not shown	M _{1RD}	M _{1RD}
4	M _{1RV}	M _{1RV}
3	M _{2R}	—
	M _{3R}	M _{2R}
2	M _{4R} bucco-pharyngeal plate	M _{3R} (bucco-pharyngeal plate bearing bucco-pharyngeal ridge)
1	M _{5R}	M _{4R}
	—	M _{5R}

M_{3L}, M_{5R}, M_{6L} and the right oral appendage of *C. elizae* are not represented in *C. curvata*. M_{2R}, M_{4L} of *C. curvata* are not represented in *elizae*.

Ventral spikes were present on M_{2R}, M_{3R} and sometimes M_{4R} (see Pl. 3, fig. 7), and on M_{2L}. These spikes are denoted respectively as S_{1R}, S_{2R}, S_{3R} and S_L.

THECAL OPENINGS: The branchial slits (Fig. 9; Pl. 3, figs. 2, 3, 4, 7) are situated much as in *C. elizae* but number about 40 and differ in structure. The slits are separated by chevron-shaped plates (interbranchial chevrons, ibc in Fig. 9) each of which fits accurately against its neighbours. The low crest of the chevron (cr) points outwards and may represent a suture, for it often fractures. Each interbranchial chevron has grooves in its sides just above the ventral margin (arcuate grooves, arg in Fig. 9). These grooves end anteriorly and posteriorly as the cavities

of hollow processes (anterior and posterior excavate processes, aep, pep in Fig. 9).

Most of the ventral surface of the chevron is occupied by a ventral groove (vg) which is widest beneath the crest of the chevron. The rest of the ventral surface is occupied by the ventral walls of the arcuate grooves except for anterior and posterior semicircular tabulate areas at the tips of the chevron.

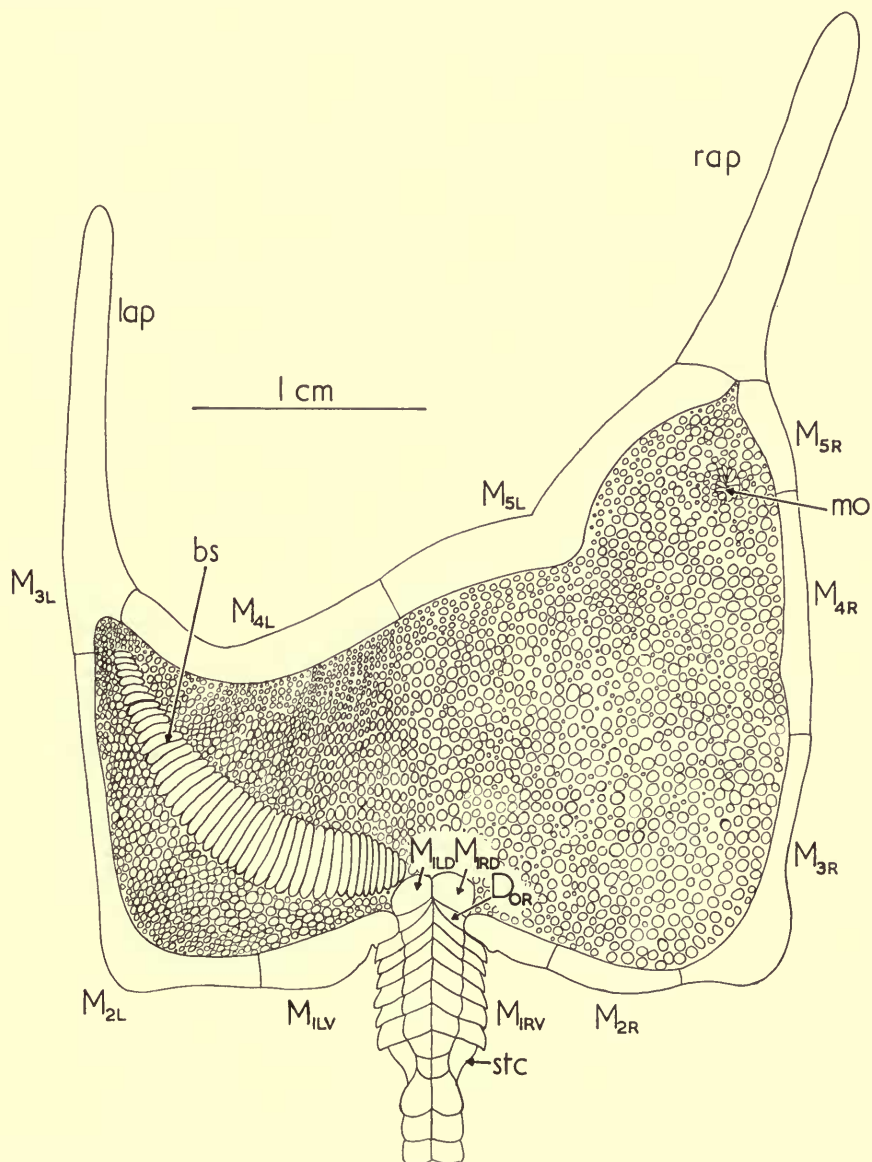


FIG. 8. *Cothurnocystis curvata*. Reconstruction of external features. a. dorsal; b. ventral; c. anterior; d. posterior; e. left; f. right aspects. bs = branchial slit; lap = left appendage; rap = right appendage; stc = stylocone; str = strut.

The branchial complex almost certainly acted as an outlet valve. It was mounted in a flexible integument. When the pressure was high beneath this integument the complex would belly out, the chevrons would separate from each other and water would escape. When the internal pressure consequently decreased the integument would deflate, the chevrons would clap together and water would be unable to enter. The crests of the chevrons would coincide with the line of greatest

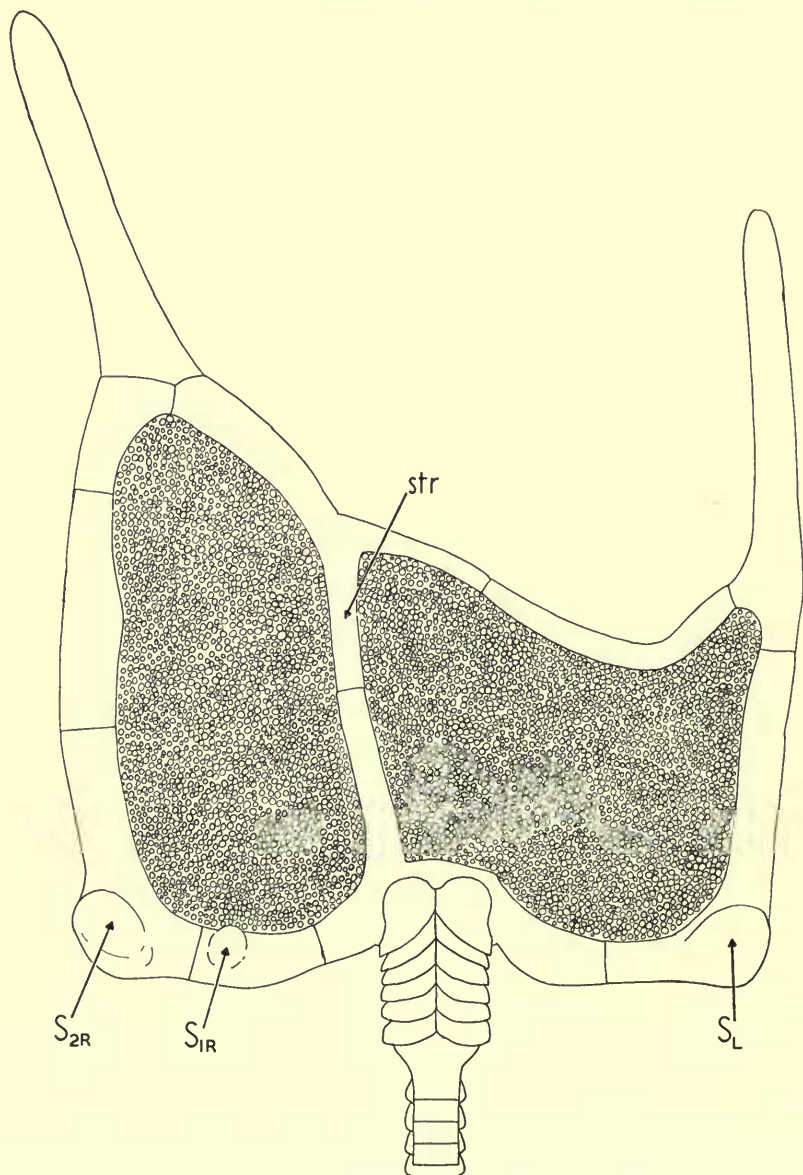


FIG. 8b.

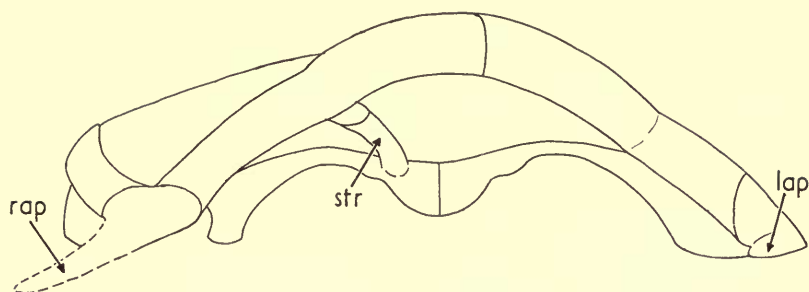


FIG. 8c.

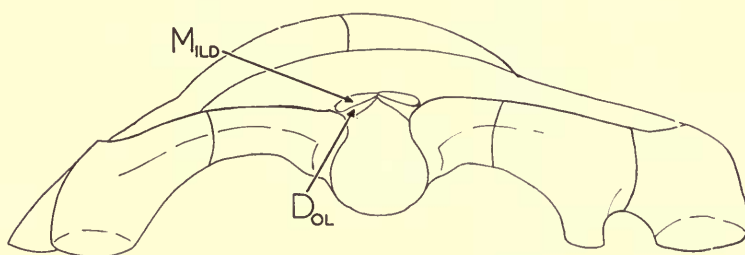


FIG. 8d.

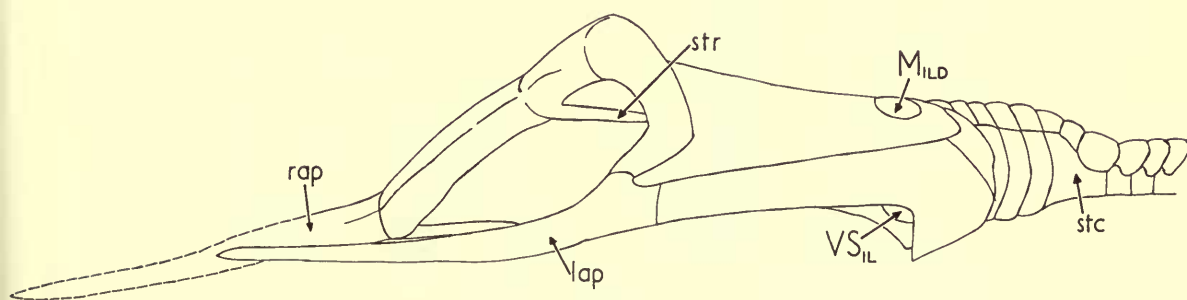


FIG. 8e.

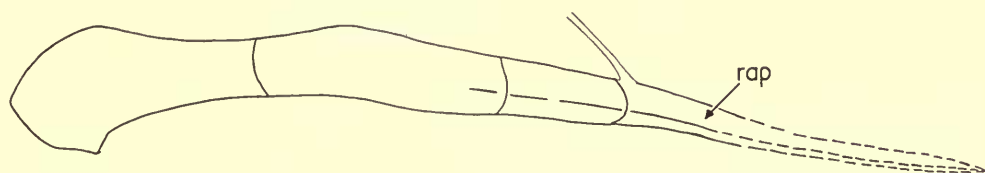


FIG. 8f.

stretching of the integuments, and this would increase the efficiency of the valve mechanism.

Each arcuate groove was probably filled with connective tissue, which may have projected slightly out of the groove when the chevrons were separate. It would consequently press against the contents of the neighbouring arcuate groove when the

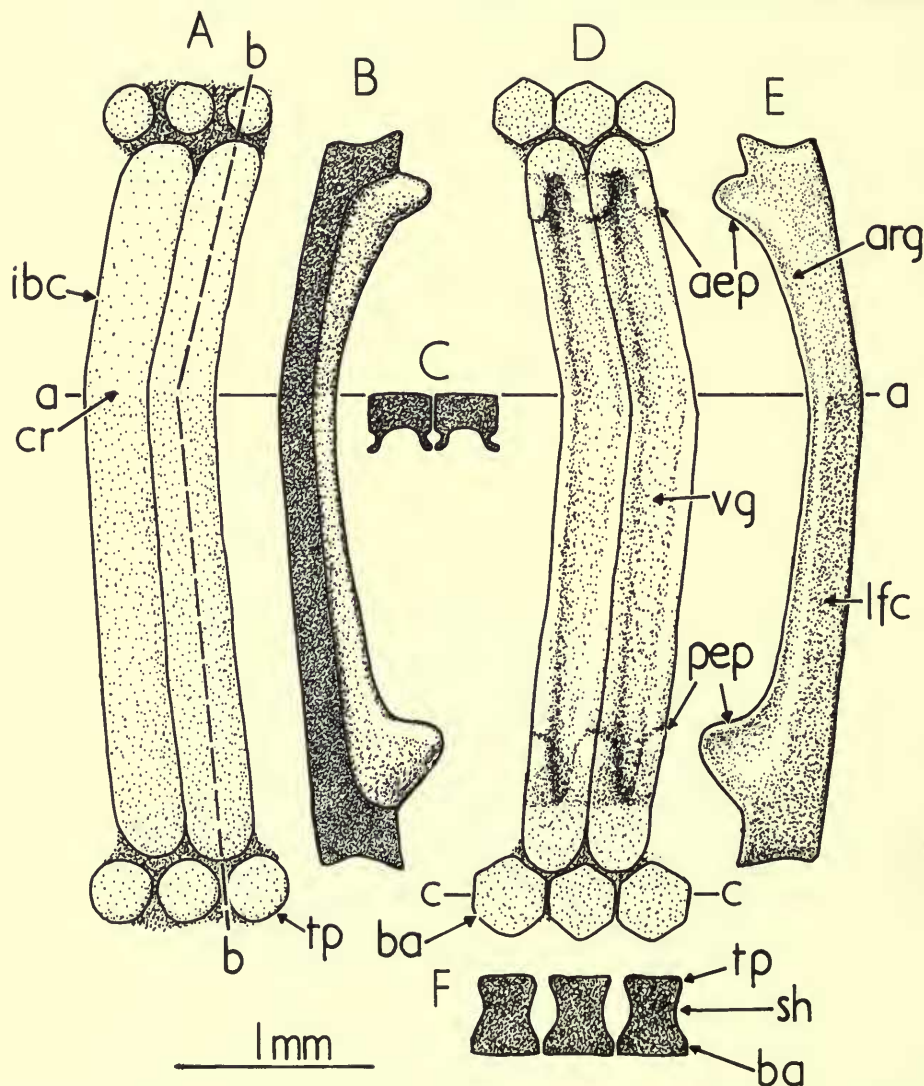


FIG. 9. *C. curvata*. Branchial skeleton. A. External aspect; B. longitudinal section through b-b; C. transverse sections through a-a; D. internal aspect; E. left lateral aspect; F. Section through plates of integument c-c. aep = anterior excavate process; arg = arcuate groove; ba = base; cr = crest; ibc = interbranchial chevron; lfc = lateral facet; pep = posterior excavate process; sh = shaft; tp = top; vg = ventral groove.

chevrons clapped together. This would provide an excellent seal which would increase the efficiency of the valve. The facts that: (i) the length of an arcuate groove coincides exactly with the extent to which neighbouring chevrons touch each other, (ii) the edges of an arcuate groove match exactly against those of its neighbour, (iii) the ventral positions of the grooves coincide with the parts of the chevrons that would first come together on deflation, strongly confirm this interpretation.

By comparison with *C. elizae* each chevron represents the fusion of adjacent halves of neighbouring anterior and posterior u-plates. The presumed crestal suture of *C. curvata* represents the articulation between anterior and posterior u-plates of *C. elizae* and also a corresponding suture through the branchial slits of *Ceratocystis perneri*. The branchial valve mechanism of *C. elizae* depended on the bellying-out of the integuments under pressure, the bending of the frames of the slits, and the flexibility of the flaps. The branchial valve mechanism of *C. curvata* depended only on the bellying-out of the integument.

There is no external anus in *C. curvata* (Fig. 8a; Pl. 3, figs. 9, 10). An obvious rectal groove (rg in Fig. 11a; Pl. 3, fig. 5) runs across the floor of the posterior coelom but, instead of opening directly to the outside, joins a distal rectal canal (drc in Fig. 11a; b; Pl. 3, fig. 9) in M_{ILD} running anteriorly and dorsally. This canal leaves M_{ILD} where only a small stretch of integument separates it from the most median interbranchial chevrons. The anus must therefore have been internal, opening into the most median branchial slits, downstream of any food-collecting surface inside the pharynx.

The outlet current from the gill slits of *C. curvata* would be perpendicular to the integument, instead of horizontal and backwards as in *C. elizae*. A very close association of branchial slits and anus would therefore be advantageous. This close association proves that the distal rectal canal was indeed an outlet and confirms the identification of the anus in *C. elizae*.

The mouth was surrounded by pointed plates, as in *C. elizae*, but was dorsal in position. This involves no difference in the "connections" with the surrounding skeleton, for even in *C. elizae* a lower lip separates the mouth from the nearest parts of the marginal frame (M_{6L} and M_{5R} in *C. elizae*).

The dorsal position of the mouth shows that *C. curvata*, unlike *C. elizae*, was a suspension rather than a deposit feeder. This explains a number of other differences from *C. elizae*, viz: 1. the absence of the right oral appendage, which in *C. elizae* was specialized in connection with deposit feeding, 2. The narrowness of the rectal groove, which would not need to carry much mineral detritus. 3. The possible loss of powers of movement in the adult (see p. 277), since there would be no need to graze the sea floor.

THE CHAMBERS OF THE THECA: A buccal cavity corresponding to that of *C. elizae* is indicated by: (i) the gross separation of "ankle" and "foot" region, visible externally, (ii) the presence of a dorso-ventral ridge (rbcr) on the inside of M_{4R} (Pl. 3, figs. 2, 7), just opposite the sharp angle (rbcl) in M_{5L} between "foot" and "ankle" regions, (iii) gaps between the attachment facets of dorsal and ventral integuments visible on the internal cast both to right and left of the "ankle" region.

These gaps are widest in the middle of the region and diminish and disappear both anteriorly and posteriorly (Fig. 10a, b, d; Pl. 4, figs. 2, 3). They suggest a definite chamber between the integuments in this area.

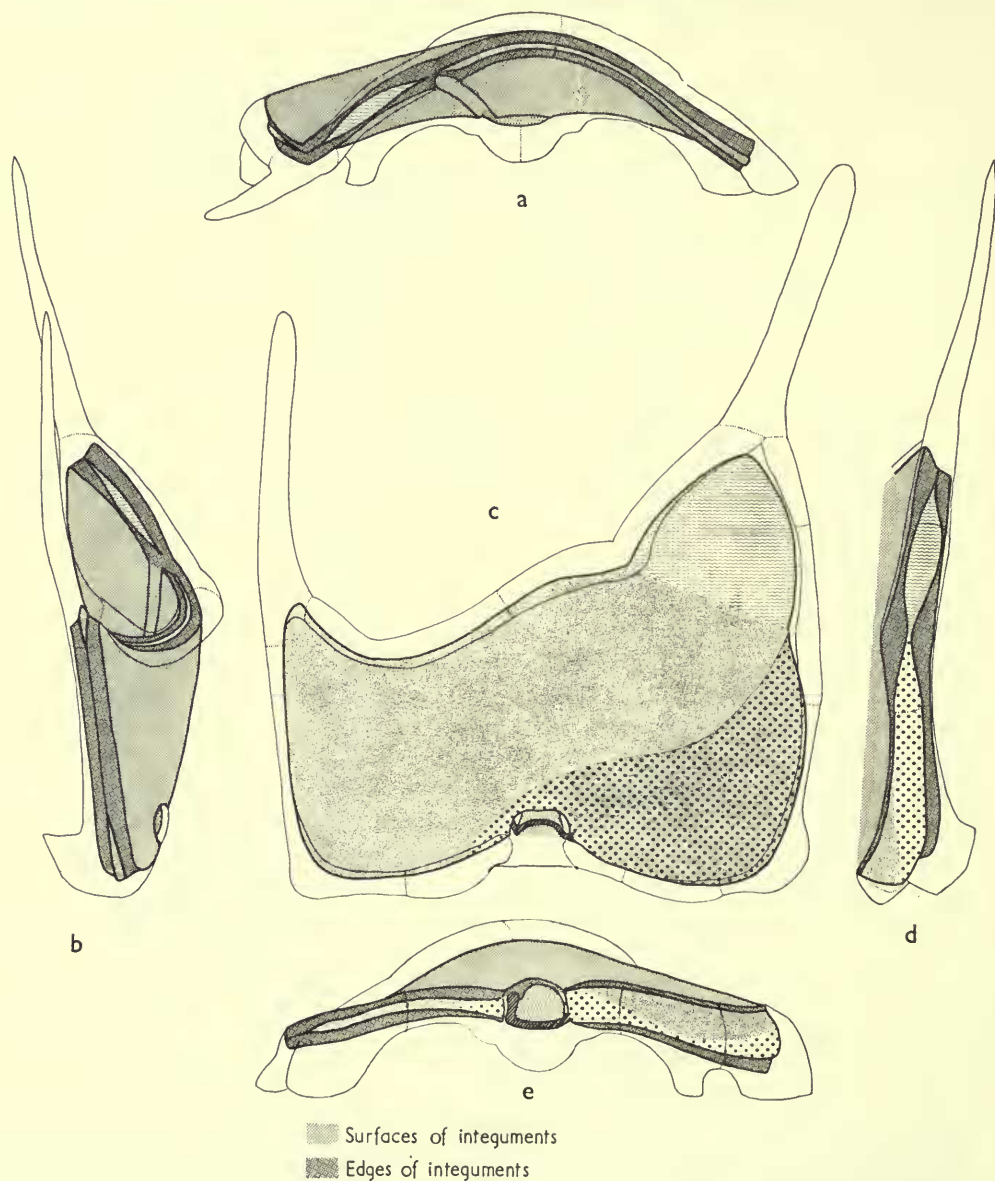


FIG. 10. *C. curvata*. Chambers of theca. a. anterior; b. left; c. dorsal; d. right; e. posterior aspects. Skeleton assumed to be transparent and, except in 10c, the integuments assumed to be opaque. Stipple of chambers as in Text-fig. 14.

The posterior coelom (pco in Fig. 11a; Pl. 3, figs. 2, 5) shows more clearly than in *C. elizae*. It is floored by the dorsal faces of M_{ILV} and M_{IRV} , roofed over by the ventral faces of M_{ILD} and M_{IRD} and defined antero-ventrally by antero-ventral processes (avp) of the latter, which rest directly on M_{ILV} and M_{IRV} . The posterior coelom lay in front of the brain and the rectum ran in the rectal groove (rg) beneath it.

The positions of anterior coelom and pharynx cannot be deduced directly from the superficial internal anatomy. As in *C. elizae*, however, the anterior coelom probably lay mainly in the posterior, right-hand part of the theca, since the rectum

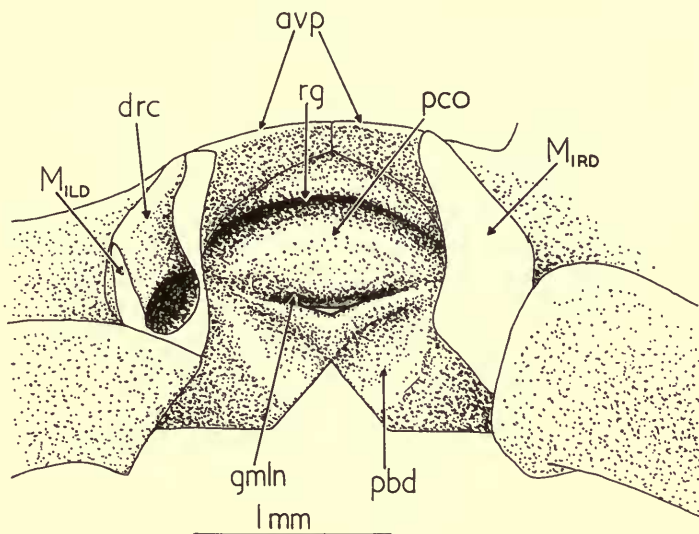


FIG. 11. *C. curvata*. Structure of region just anterior to stem. a. dorsal aspect, with most of M_{IL} and M_{RD} removed; b. anterior; c. posterior aspect. avp = antero-ventral processes of M_{IL} and M_{RD} ; ceb = cerebral basin; cmln = canal for median-line nerves; drc = distal rectal canal; gmln = groove for median-line nerve; pbd = depression for pyriform bodies; pco = posterior coelom; rg = reception groove for anterior stem; rf = rectal foramen; rg = rectal groove.

entered the posterior coelom from this region and the space between the integuments is much deeper to the right of the stem than to the left (Fig. 8d).

THE INTEGUMENTS: The plates of the integument (Fig. 9F) consist of a polygonal base (ba) internally, with a process arising from it. This process may have a constricted shaft (sh) and an expanded top (tp), or it may be hemispherical or have some intermediate shape. The polygonal base is everywhere in contact with its neighbours.

Dorsal and ventral attachment facets (uiaf and liaf) for the integuments, in most places separated by a space of varying depth, existed on the inner faces of the marginal plates (Fig. 10; Pl. 4, figs. 2, 3, 5, 6, 8).

Differentiation of the integument plates is less marked than in *C. elizae*. The plates of the ventral integument are smaller than those of the dorsal integument.

Plates with hemispherical processes are commonest in the posterior right-hand corner of the theca.

The spaces between neighbouring processes probably contained muscle. The shortness of the processes in the posterior right-hand corner therefore suggests that the plates here were less involved with pumping than elsewhere. This can be related to the probable position of the anterior coelom.

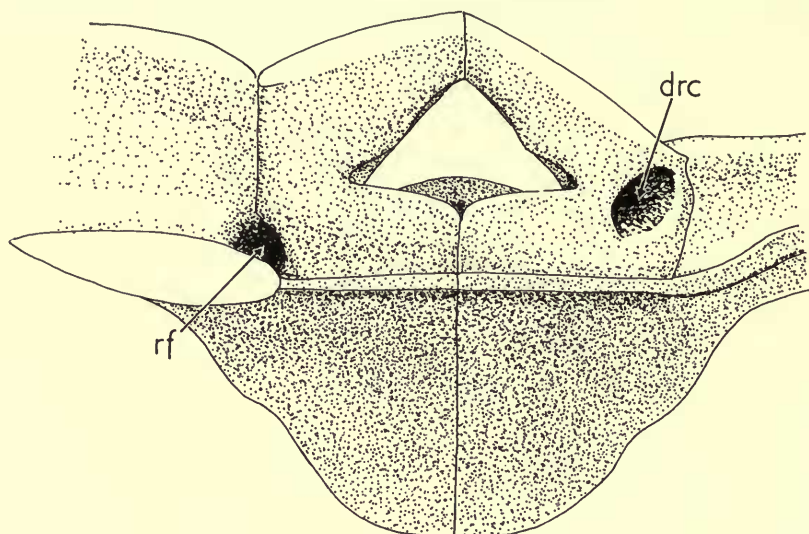


FIG. 11b.

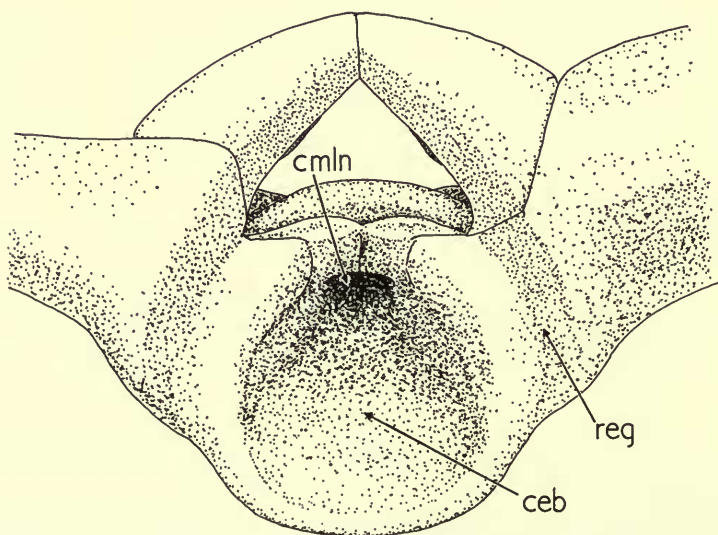


FIG. 11c.

THE STEM: The posterior stem is incomplete in all the larger specimens studied. In E 28661, whose maximum width across the theca was 18 mm., it must have contained more than sixteen segments. The number of segments increased in ontogeny for in E 28552 (thecal width = 6.5 mm.) there are only nine segments in

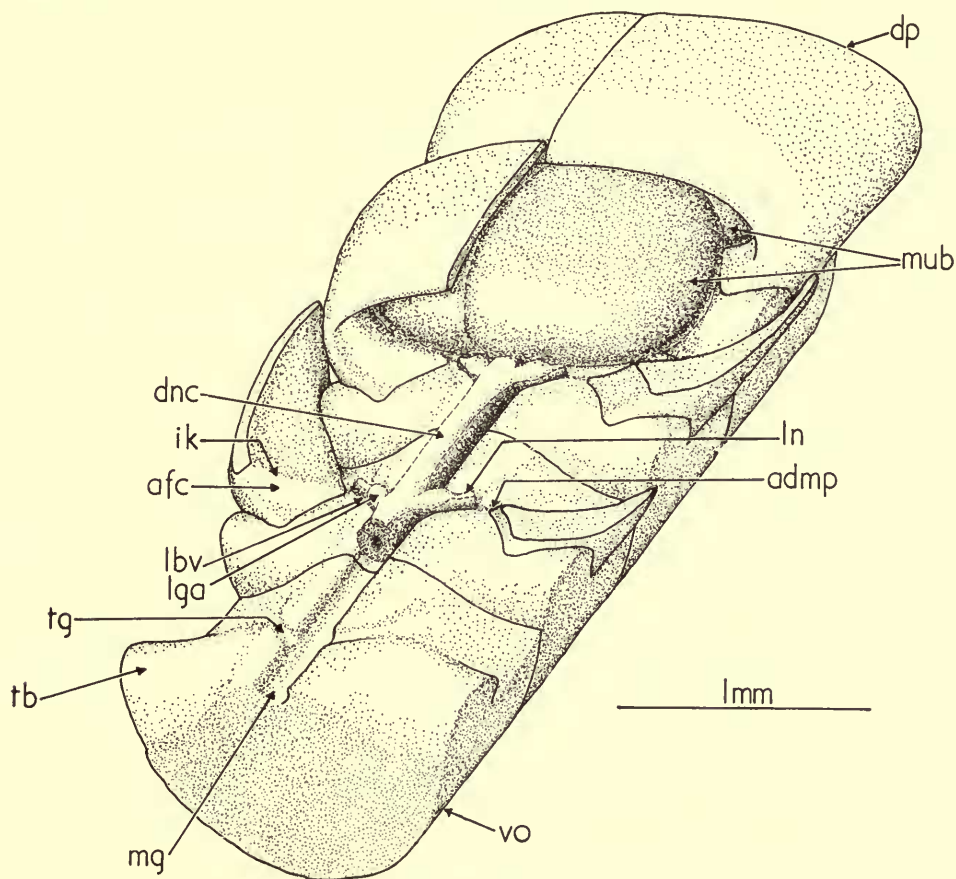


FIG. 12. *C. curvata*. Block diagram of portion of posterior stem. admp = admedian process of dorsal plate; afc = anterior facet of dorsal plate; dnc = dorsal nerve cord; dp = dorsal plate; ik = internal keel of dorsal plate; lbr = lateral blood vessel; lga = lateral ganglia; ln = lateral nerve; mg = median groove; mub = muscle blocks; tb = transverse buttress; tg = transverse groove; vo = ventral ossicle.

the whole posterior stem. As in *C. elizae* the stem, when complete, seems to have ended abruptly.

The structure of individual segments is basically (Fig. 12; Pl. 4, figs. 1, 4) as in *C. elizae*. There was a hemicylindrical ventral ossicle (vo) and a pair of dorsal plates (dp). The dorsal surface of the ventral ossicle carried a median groove (mg) which gave rise to a pair of transverse grooves (tg) running obliquely backwards. Unlike *C. elizae*, the anterior half of the dorsal face of each ventral ossicle carried

paired, hemicylindrical, transverse buttresses (tb). The dorsal plates were thicker than in *C. elizae* and there is an internal keel (ik) separating an anterior internal facet (afc) from the rest of the internal surface of the plate. The internal keel ends ventrally in an admedian process (admp). The interface between a ventral ossicle and a dorsal plate is of large area and complicated shape, straddling the transverse buttress and part of the dorsal surface of the same ossicle behind the buttress.

As regards interpretation, it is clear, firstly, that the dorsal plates, because of their complicated ventral articulation, could not have opened outwards as Prof. Ubaghs' hypothesis would require. Secondly, the space between dorsal plates and ventral ossicles, which would be largely filled with muscle, is partially subdivided by the admedian processes and internal keels of the dorsal plates. This partial subdivision probably indicates the division between muscle blocks (mub) as shown in Fig. 12. Thirdly, the transverse grooves, which probably carried lateral blood vessels (lbv) ventrally, with lateral nerves (ln) and ganglia (lga) overlying, must have run between the muscle blocks if these were arranged as suggested. In this they resembled the ganglia and probable lateral blood vessels of mitrates. The posterior stem was probably stiffer in life than that of *C. elizae* for it is relatively stouter, the faces between the ossicles are all exactly plane, and there was relatively less space for muscles.

The medial stem of *C. curvata* differs from that of *C. elizae* in having three segments, indicated by three pairs of dorsal plates, instead of two. It also has a very abrupt posterior taper, especially dorsally.

The anterior stem is offset ventrally to the theca to an even greater degree than in *C. elizae* (Fig. 8d). It has about six segments, each containing right and left, dorsal and ventral plates as in *C. elizae*. All the plates of a ring imbricate everywhere beneath the corresponding plates of the ring next in front. This would give flexibility dorso-ventrally as well as laterally. The anterior ventral plates (VS_{1L} and VS_{1R}) fit dorsally in a reception groove in M_{1LV} and M_{1RV}. More ventrally they overlap these two plates, which again would allow vertical flexion. Between the dorsal plates D_{1L} and D_{1R} and M_{1LD} and M_{1RD} two small triangular plates (D_{0L} and D_{0R}) are inserted as in *C. elizae*, without ventral plates corresponding.

The anterior stem would need some anticompressional structure (notochord or chambered organ) to prevent telescoping, since compressional stresses would be taken up by the skeleton even less than in *C. elizae*. A nerve cord, powerful muscles, presumably in blocks, and a blood supply must also have existed.

THE BRAIN: The brain is much like that of *C. elizae*. It was contained in a cerebral basin (ceb in Fig. 11c; Pl. 3, fig. 8) excavated in M_{1LV} and M_{1RV}. The median line nerves left the brain in a canal (cmln in Fig. 11c) which bifurcates away from the brain and leads to two grooves (gmln in Pl. 3, fig. 5). There are triangular depressions (pbd) for the pyriform bodies.

POSTURE AND MOVEMENT: There is no doubt that *C. curvata* lived with the dorsal side uppermost since, as in *C. elizae*, all the openings are dorsal and all processes are ventral.

The habitual direction of movement must have been backwards as in *C. elizae*.

This is shown by the anterior appendages, which dip downwards anteriorly, and the spikes S_{1R} , S_{2R} , S_{3R} and S_L which are truncated by oblique planes, dipping downwards anteriorly (Fig. 8e, f). The theca is more symmetrical than in *C. elizae*, however, and the habitual direction of movement, parallel to the anterior appendages, must have been more directly backwards.

The stem cannot have acted exactly as in *C. elizae*, for the anterior stem could flex up and down, as well as sideways, and the posterior stem was probably relatively stiff. The prominent anterior appendages would have prevented yawing, and suggest that the animal, like *C. elizae*, pulled itself along by side-to-side movements of the stem. The sequence was probably as follows: the posterior stem was stuck obliquely into the sea-floor, somewhat to the left, by the action of the anterior stem; the stem bent still more to the left, pulling the theca backwards; the posterior stem was pulled out of the sea-floor; the stem bent slightly to right and the sequence was repeated on the right side.

Movement may not have been habitual in the adult, since most large specimens have lost the oral appendage and all the posterior stem except two or three segments.

c. *Mitrocystella incipiens* (Barrande) *miloni* Chauvel

SYSTEMATIC POSITION: Phylum: Chordata. Subphylum: Calcichordata. Class: Stylophora Gill & Caster 1960. Order: Mitrata Jaekel 1918. Family: Mitrocystitidae Jaekel 1900 (as Mitrocystidae). Genus: *Mitrocystella* Jaekel 1900. Species: *Mitrocystella* [*Anomalocystites*] *incipiens* (Barrande 1887). Subspecies: *Mitrocystella incipiens miloni* (Chauvel 1941).

OCCURRENCE: The subspecies occurs in siliceous nodules in the "Schistes à Calymènes" (Ordovician, Llandeilo Series) of Brittany. The main locality is le Grand Champ de Traveusot, Ille-et-Vilaine (Chauvel 1941: 176). *Mitrocystella incipiens incipiens* occurs in the Šárka Beds (Llanvirn Series) of Bohemia, but is usually ill-preserved. The associated fauna of trilobites, brachiopods and molluscs indicates a shallow-water, marine environment.

MATERIAL: About 280 specimens in the Institut de Géologie, Rennes (mainly Milon Coll.); A 46271 in the Sedgwick Museum, Cambridge (MacGregor Coll.); two specimens in the Department of Geology, University of St. Andrews, Scotland (MacGregor Coll.); and seven specimens E 23664-5 and E 23885-9 in the British Museum (Natural History) (Chauvel Coll.).

Certain points of interest were seen in *Mitrocystella incipiens incipiens* from Bohemia. Three of the specimens studied are in the British Museum (Natural History) E 23606-8 and six in the Museum of Comparative Zoology, Harvard (580-5). A large number are also preserved in the Národní Museum (Prague), but of these only one, in a siliceous nodule (Acc. cat. 22011, Inv. no. 688, Šárka Beds ($\delta\gamma_2$), loc. Šárka, coll. Hanuš) was informative.

GENERAL SHAPE AND PLATE NOMENCLATURE: The thecal skeleton of *M. i. miloni* consists of two parts (Fig. 13a, b). There is a shield of large plates forming what is here regarded as the dorsal side ("plastron" (Caster 1952), "face inférieure")

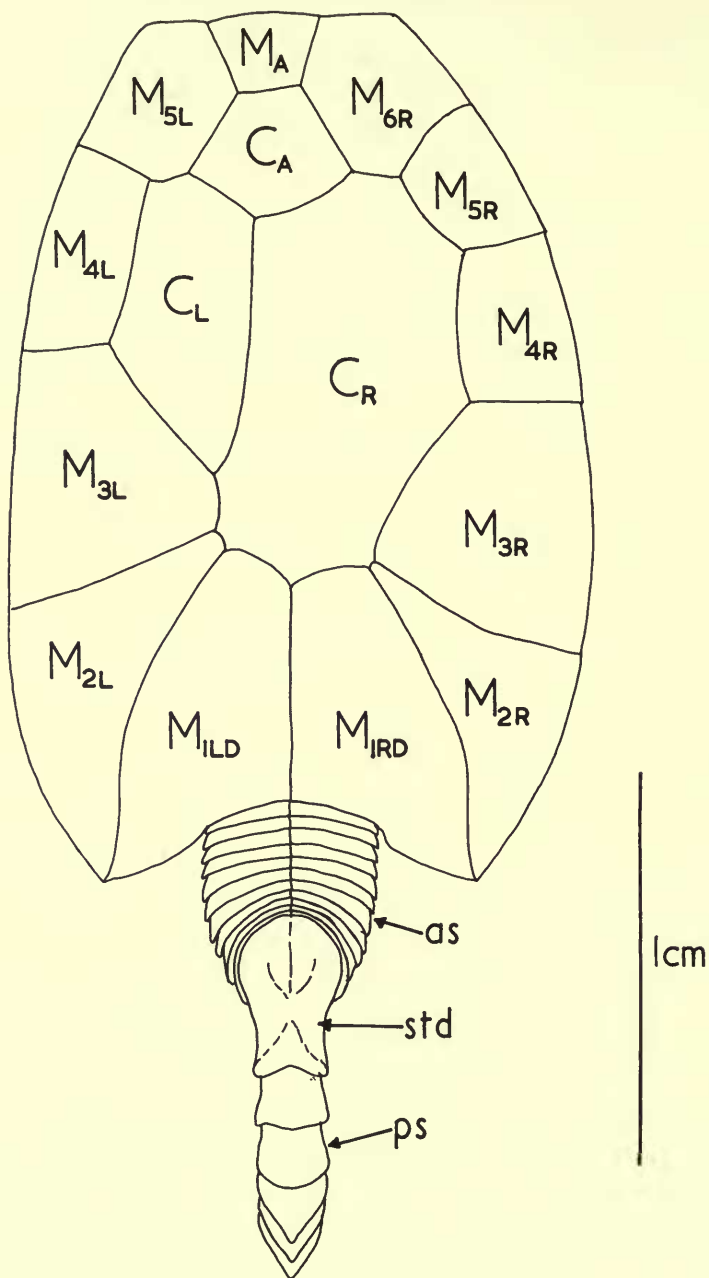


FIG. 13. *Mitrocystella incipiens miloni*. a. dorsal ; b. ventral ; c. right ; d. anterior ; e. posterior aspects. as = anterior stem ; bo = branchial opening ; ia = interossicular articulation ; mo = mouth ; ng = narrow groove (lateral line) ; or = oral plate ; ps = posterior stem ; std = styloid ; tr = transverse ridge ; vp = ventral plate of posterior stem ; x = point where a ventral plate imbricates over a dorsal ossicle.

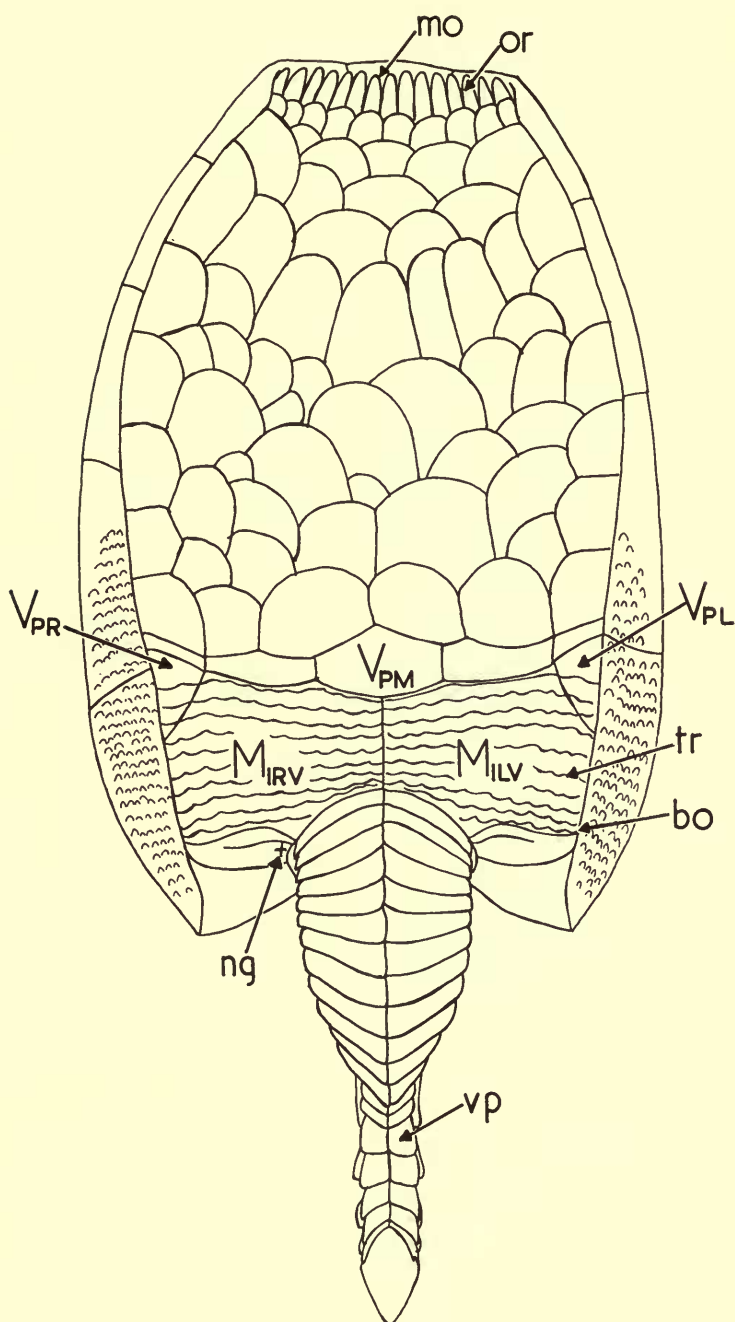


FIG. 13b.

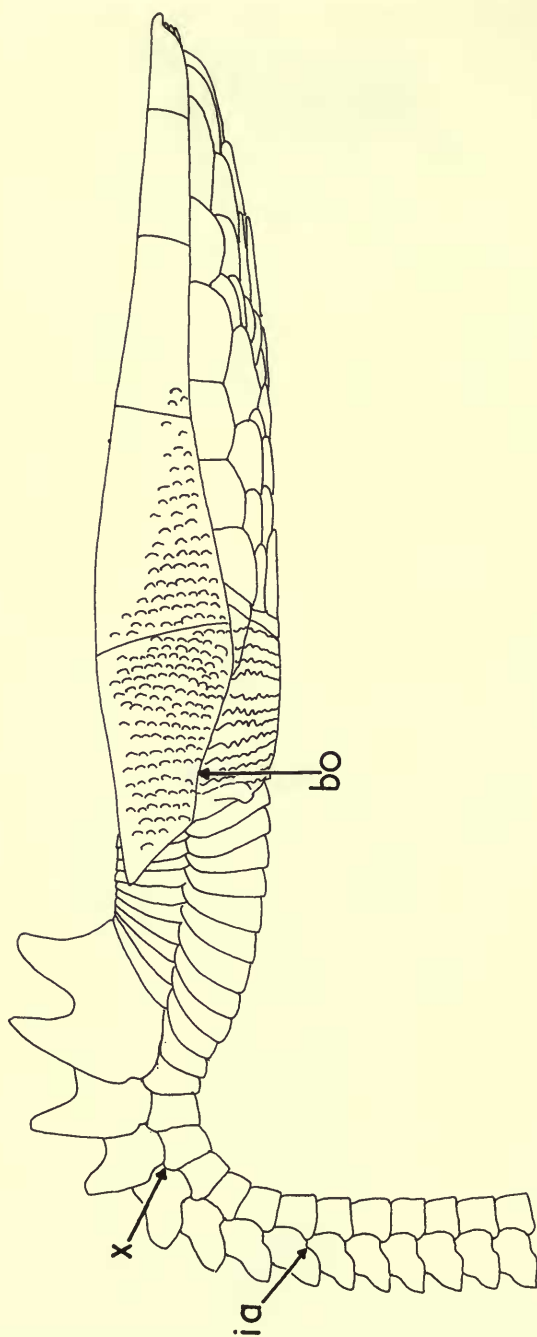


FIG. 13c.

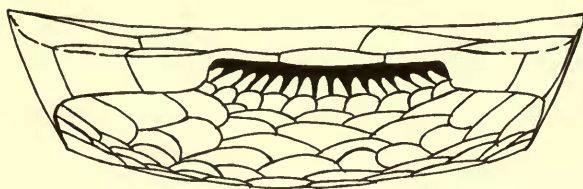


FIG. 13d.

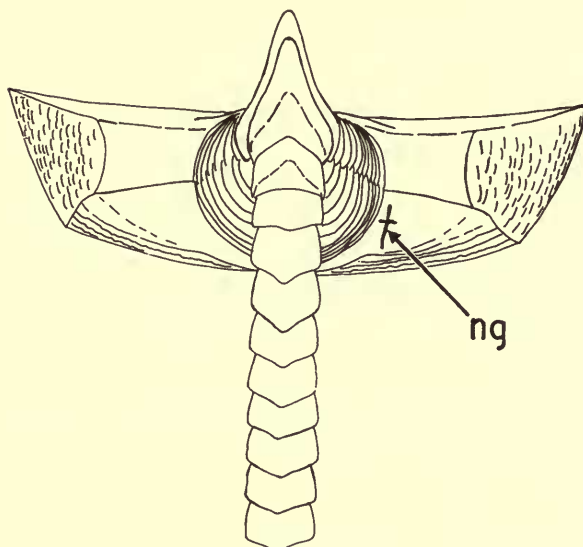


FIG. 13e.

(Chauvel 1941), "Dorsalseite" (Jaekel 1900), "Unterseite" (Jaekel 1918), "reverse side" (Gislén 1930)). The ventral face ("carapace" (Caster 1952)) was evidently more flexible except posteriorly.

The plates present in the theca are as follows:

Notation	Name	Chauvel 1941
M _{1LD}	Left dorsal 1st marginal	M 1° marginale droite
M _{1LV}	Left ventral 1st marginal	I + E Interbasale and épibasale
M _{2L}	Left 2nd marginal	M ₂ 2° marginale droite
M _{3L}	" 3rd "	M ₃ 3° " "
M _{4L}	" 4th "	M ₄ 4° " "
M _{5L}	" 5th "	M ₅ 5° " "
M _A	Anterior marginal	M ₆ 6° " "
M _{1RD}	Right dorsal 1st marginal	M _{1'} 1° marginale gauche
M _{1RV}	Right ventral 1st marginal	I + E Interbasale and épibasale
M _{2R}	" 2nd marginal	M _{2'} 2° marginale gauche
M _{3R}	" 3rd "	M _{3'} 3° " "

Notation	Name	Chauvel 1941
M _{4R}	„ 4th „	M ₄ ' 4° „ „
M _{5R}	„ 5th „	M ₅ ' 5° „ „
M _{6R}	„ 6th „	M ₆ ' 6° „ „
C _L	Left central	H ₂ 2° hypocentrale
C _A	Anterior central	H ₃ 3° „ „
C _R	Right central	H ₁ 1° „ „
—	Ventral plates	épicales
V _{PM}	Median posterior ventral	No special name
V _{PL}	Left posterior ventral	„ „ „
V _{PR}	Right posterior ventral	„ „ „

Chauvel's scheme, and to a lesser extent the one adopted here, is based on that of Jaekel (1918), with additions. The plates just anterior to the stem, i.e. M_{1LV}, M_{1LR}, M_{1LD} and M_{1RD}, must be homologous with the like-named plates in cornutes. The homologies of the other plates are unclear, except that the marginals must be broadly homologous with those of cornutes.

The stem is divided into anterior, medial and posterior parts as in the cornutes. Details of the stem skeleton are given below (p. 289).

THECAL OPENINGS: The mouth (mo in Fig. 13b) faces slightly leftwards (cf. p. 314). It is bordered above by part of the rigid dorsal shield (M_{6R}, M_A, M_{6L}) and below by about fifteen elongate oral plates (or). These are fixed to a flexible lower lip, studded with post-oral plates, which is dorsal to the front edge of the ventral armour.

The rigid skeleton above the mouth of *M. i. miloni* contrasts with the situation in *Cothurnocystis elizae* where the skeleton was rigid beneath the mouth. An intermediate situation exists in the earliest known mitrocystitid (*Chinianocarpus thoralis* Ubahgs from the Upper Tremadoc or Lower Arenig Series of the Montagne Noire), where the mouth is entirely surrounded by large plates, i.e. M_A dorsally, M_{5R} and M_{5L} ventrally (Ubahgs 1961a and personal observation).

There are no external branchial slits in *M. i. miloni*. Paired, external, branchial openings (bo in Figs. 13b, c, 15H) seem to have existed, however, near the posterior right- and left-hand corners of the theca. The roughly horizontal suture between M_{1D} and M_{1V} on each side is curved (Fig. 15I) as if to facilitate articulation (cf. Fig. 7) about the length of the suture. When M_{1V}, because of high pressure inside the theca, rocked backwards on this suture, an opening would appear between it and M₂, and close again when M_{1V} rocked forwards as the pressure fell. The opening would thus behave as an outlet valve. It would be faced on both sides almost entirely by the connective tissue of the middle layer of the skeleton (Fig. 15H) which would provide a seal like that round the branchial slits of *C. curvata*. The nerve n₃ (optic) ran just anterior to the opening while n₄ ran just median to it. The branchial openings rested on the substratum but the analogy of modern rays and skates shows that they could have functioned in this position. *M. mitra* (p. 314) had similar branchial openings which are in some ways easier to interpret.

There was no external anus in *M. i. miloni*, as discussed below (p. 287).

A narrow vertical groove on M_{1RV} (ng in Fig. 13b, c; Pl. 4, fig. 9) is here regarded as a rudimentary lateral line (cf. p. 307, below). It sometimes has a short horizontal groove across it (Pl. 9, fig. 4).

THE CHAMBERS OF THE THECA: A direct picture of the chambers of the theca (Fig. 14a, b) can be obtained from the internal cast, whose surface is traversed by grooves which separate the original chambers and correspond to ridges on the skeleton.

A groove (oblique groove), running from near the right side of the mouth to near the left side of the stem, is the most notable feature of the dorsal side of the internal cast. This groove ("sillon transversal" of Chauvel 1941) is not symmetrical in section. For most of its length it is steeper to the right than to the left so that it grossly separates a left, anterior, ventral chamber from a right, posterior, dorsal chamber.

The oblique groove is here held to be broadly homologous with the pharyngo-visceral line of *Cothurnocystis elizae*. The chamber anterior and to the left of it corresponds to the pharynx of *C. elizae* and is henceforth called the left pharyngeal chamber. The chamber posterior to, and to the right of, the oblique groove is broadly homologous with the anterior coelom of *C. elizae*, apart from some complexities which are discussed below.

The oblique groove is flexuous and varies in strength. Anteriorly it bays out to the right. For a short distance in the anterior part of this embayment the left side of the groove is steeper than the right side (Fig. 15A; Pl. 5, figs. 7, 9). Here, therefore, the left pharyngeal chamber overlay the anterior coelom. In the middle of the embayment the groove is shallow and symmetrical (Fig. 15B; Pl. 5, figs. 1, 7, 9). In the posterior part of the embayment it deepens, has a rounded floor, and is steeper to right than to left (Fig. 15C). Behind the embayment the groove sends out a median branch (mb in Pl. 9, fig. 2). This is triangular in section (Fig. 15D), tapers posteriorly, and is largely hidden in the internal cast. For a short distance behind and left of the separation of this median branch the oblique groove again has a rounded floor and is symmetrical (Fig. 15D; Pl. 9, fig. 2) or has the right side only a little steeper than the left. Behind this the floor of the groove suddenly becomes angular (at point v in Pl. 9, fig. 2), with the right side distinctly steeper than the left (Fig. 15E). The depth, angularity and asymmetry of the groove increase gradually backwards (Fig. 15F). Posteriorly the oblique groove gives rise to two other grooves. The left one of these runs backwards and then vertically downwards while the other ("sillon pedonculaire" of Chauvel 1941) turns to the right.

The anterior embayment and weakening of the oblique groove suggest an outpouching from the left pharyngeal chamber. This outpouching is henceforth called the right pharyngeal chamber; in ontogeny it must have pushed the anterior coelom upwards and partly obliterated its lumen.

The median boundary of the right pharyngeal chamber is indicated anteriorly by the median branch of the oblique groove and more posteriorly by a very weak

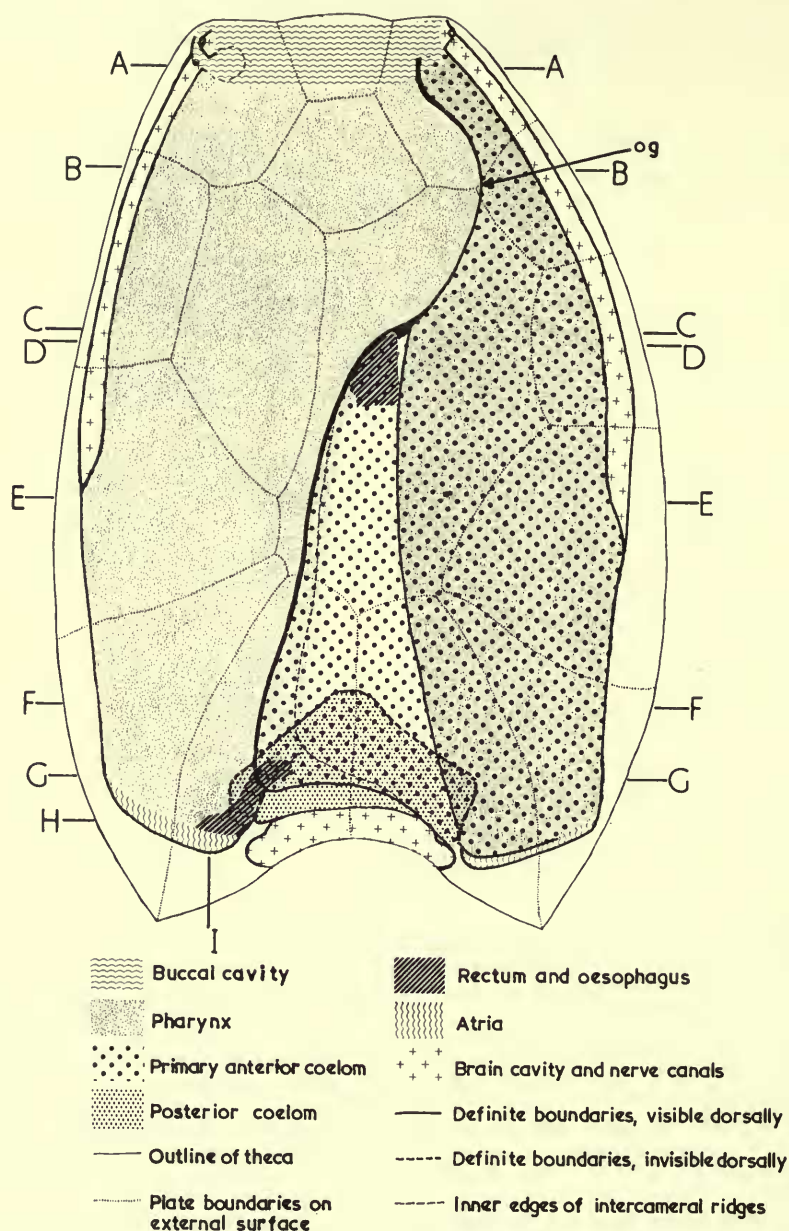
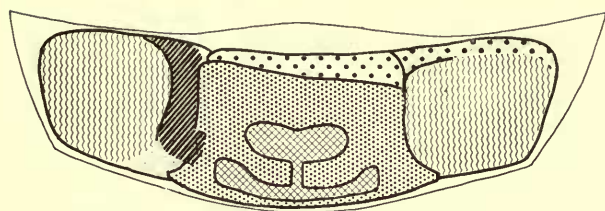


FIG. 14. *M. i. miloni*. Chambers of theca. a. dorsal; b. posterior aspects. og = oblique groove. A—A to G—G, H and I indicate planes of section used in Text-fig. 15. Stipple is used here as in Text-figs. 4 and 10.



Canals from posterior face of posterior coelom

FIG. 14b.

groove (grp in Pl. 5, fig. 1 and Pl. 10, fig. 1) running from the right side of the median branch to a point just right of the stem. This groove is weak because it does not correspond to any actual gap between chambers at the surface of the skeleton (cf. Fig. 15E, F).

In ontogeny the left pharyngeal chamber evidently preceded the right pharyngeal chamber, and it is therefore likely that the left gill slits preceded the right ones. This is what happens in the ontogeny of amphioxus (Willey, 1894, p. 130 ff.).

The rounding of the floor of the oblique groove just behind and left of the median branch may indicate that the oesophagus opened here into the left pharyngeal chamber. There are two reasons for this supposition. Firstly, the exact form of the internal cast (Pl. 9, fig. 2) suggests that some roughly cylindrical structure was in contact with the skeleton here. Secondly, by analogy with tunicates, the oesophagus should open into the pharynx in a median, dorsal position. Comparison with tunicates is reasonable on account of the disposition of the rectum, as discussed below.

The posterior coelom (pco) is delimited by the above-mentioned, right and left posterior grooves arising from the oblique groove. These sweep round the posterior coelom and meet ventrally.

The right posterior groove corresponds dorsally to Chauvel's "sillon pedonculaire". The dissection shown on Pl. 5, fig. 10, shows the oblique ridge (obr, i.e. the skeletal filling of the oblique groove) curving round gradually into the ridge filling this "sillon pedonculaire" (rpco). The exposed surface of the oblique ridge in this dissection consists of skeleton deposited against the limiting membrane of the left pharyngeal chamber. The exposed surface of the ridge (rpco) consists of skeleton deposited against the limiting membrane of the posterior coelom. The smooth connection between these two ridges in the dissection suggests that these membranes were, in fact, one and the same. The same dissection also suggests that the leftward limit of the posterior coelom (llpc), i.e. the left posterior groove arising from the oblique groove, was a fold in this membrane increasing in sharpness posteriorly. It follows that the posterior coelom became constricted off during ontogeny from the left pharynx when left pharynx and anterior coelom were already separate entities. This mode of origin of the posterior coelom is reminiscent of the origin of an epicardium in a tunicate, and it is noteworthy that Berrill (1955 : 101) regarded epicardia as homologous with coeloms. The groove on the internal cast

to the left of the posterior coelom is almost interrupted, towards its ventral end, by a bridge (rb in Pl. 5, fig. 4) whose significance is discussed below.

Two further chambers (Fig. 14a, b; ra in Pl. 9, fig. 1), situated right and left of the posterior coelom, must represent atria, for they lie between the gill openings and the presumed positions of the internal gill slits. The atria are distinctly unsymmetrical and the right one touches the posterior coelom along its whole median border. The left one, on the other hand, does not touch the posterior coelom, from which it is separated by a vertical hemicylindrical ridge (rr in Pl. 5, fig. 4) on the internal mould. This ridge connects ventrally with the bridge (rb) across

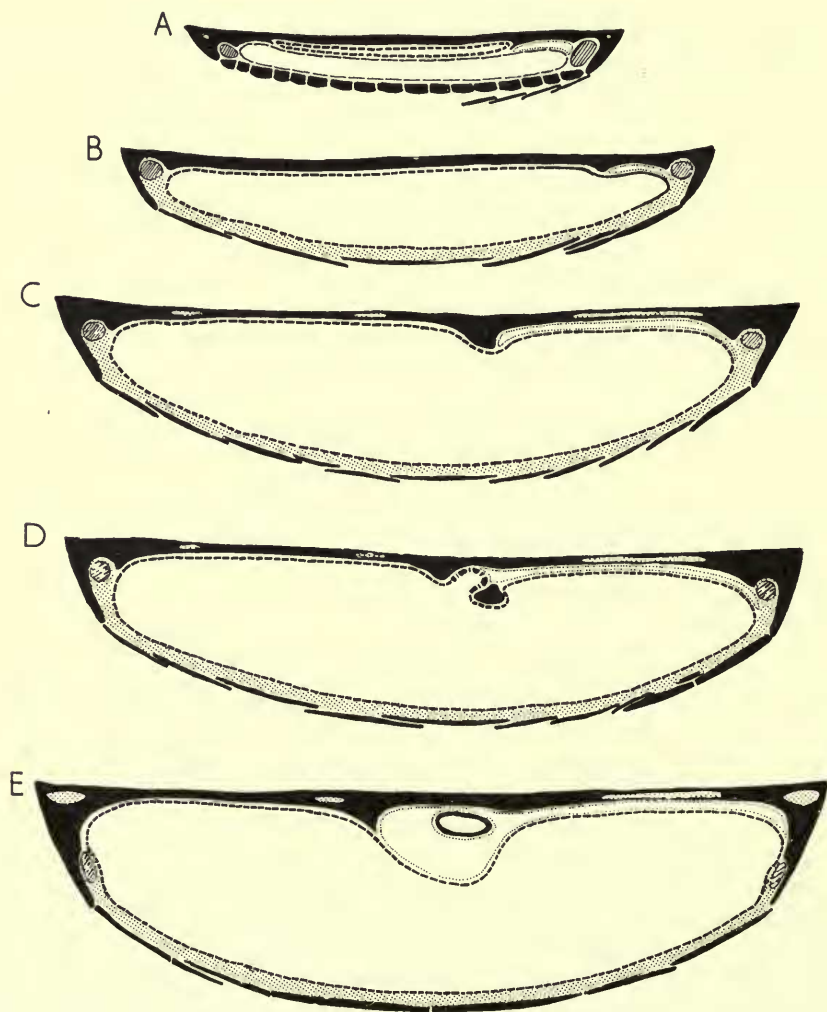


FIG. 15. *M. i. miloni*. Sections through theca to show disposition of membranes limiting chambers, and other features of the soft anatomy. bo = branchial opening.

the groove to the left of the posterior coelom. Both atria are delimited dorsally in some specimens by weak, horizontal grooves on the internal mould.

By analogy with *Cothurnocystis elizae* and *C. curvata* the rectum probably left the posterior coelom near the ventral, left posterior corner of the latter, i.e. by the bridge rb. Again by analogy with *C. elizae* and *C. curvata*, the rectum then ran vertically upwards, i.e. along the ridge rr, and must then have opened into the left atrium. Faeces would be washed away by the current through the left gill slits almost exactly as in *C. elizae* and *C. curvata*, and would finally leave the theca through the left gill opening.

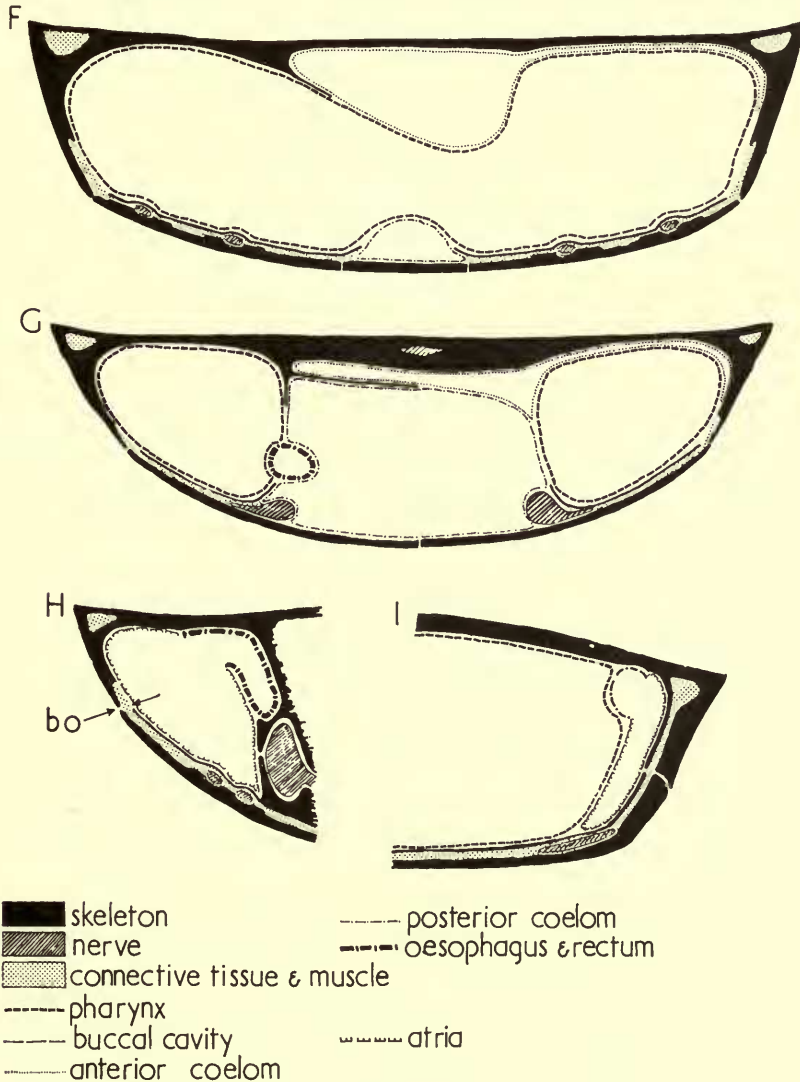


FIG. 15, F-I.

In a similar way the rectum of a tunicate tadpole either opens into the left atrium, or its closed end touches the left atrium, to open there after metamorphosis (Fig. 16; Julin 1904; Grave 1921, 1944; Kowalevsky 1867, 1871; Garstang 1928).

The existence of a buccal cavity shows clearly on the internal moulds of several specimens (bc, Pl. 5, fig. 7) just left of the mouth, where it evidently touched the dorsal skeleton (M_{5L}). Its wall was lightly calcified near the contact with the dorsal skeleton and can be followed by dissection a short way into the internal cast (Pl. 5, fig. 9). No similar structure can be found right of the mouth where the buccal cavity was probably separated from the skeleton by the pharynx and anterior coelom (Fig. 15A). The broad shape of the internal mould is the same, however, suggesting that the buccal cavity affected the dorsal skeleton without actually touching it. The relationship of the oblique groove with the buccal cavity

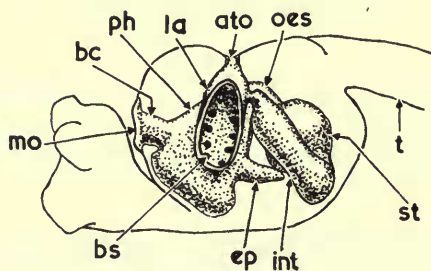


FIG. 16. Alimentary canal of the tadpole larva of the tunicate *Clavelina rissoana*, left aspect, redrawn after Julin (1904, fig. 12). ato = atrial opening; bc = buccal cavity; bs = branchial slit; ep = epicardium; int = intestine; la = left atrium; mo = mouth; oes = oesophagus; ph = pharynx; st = stomach; t = tail.

of *M. i. miloni* is almost exactly like that of the pharyngo-visceral line and buccal cavity of *C. elizae*.

The thecal chambers of *M. i. miloni* and *Cothurnocystis elizae* were, therefore, basically the same. The most fundamental difference is the appearance in *M. i. miloni* of the right pharyngeal chamber, which pouched out from the primary or left pharyngeal chamber towards the posterior, right-hand corner of the theca. In so doing, the right pharyngeal chamber lifted the anterior coelom off the floor of the theca and partly obliterated its lumen. For this reason, the junction between anterior coelom and the left or primary pharyngeal chamber (oblique groove of mitrates; pharyngo-visceral line of cornutes), which runs in both cornutes and mitrates from right of the buccal cavity to left of the stem, is in mitrates fixed to the ceiling of the theca, instead of to the right, posterior side wall. Indeed, for much of its length in *M. i. miloni* it traverses a central plate, i.e. its course is across M_{1LD} , C_R , M_{5R} and M_{6R} . It is interesting to note, therefore, that in the earliest known mitrocystitid, *Chinianocarpus thorali*, the oblique groove likewise runs across the ceiling of the theca, much as in *M. i. miloni* (Ubaghs 1961a, and personal observation). In addition, variations in its depth and direction in *C. thorali* indicate that the right pharyngeal chamber already existed. On the other hand, as in *C. elizae*,

the roof of the left pharyngeal chamber is a flexible integument and the oblique groove is entirely borne on marginal plates (M_{1LD} and M_{4R}). It is as if, in phylogeny, the oblique groove of *C. thorali* had been carried forwards and leftwards by dorsal extensions of the posterior right-hand marginals.

The basically similar disposition of the chambers of the theca in mitrates and cornutes strongly indicates, contrary to most previous authors, that the big-plated side of mitrates corresponds to the dorsal side of cornutes and was uppermost in life.

Two objections to this orientation need to be dealt with. Firstly, in the earliest known lagynocystid mitrate, *Peltocystis cornuta* Thoräl from the Upper Tremadoc or Lower Arenig Series of the Montagne Noire, the oblique groove sometimes runs from anterior left to posterior right. This is a most abnormal occurrence among mitrates, however, and is unknown in Mitrocystitidae and so can be disregarded. Secondly, if the strut of cornutes were homologous with the ridge filling the oblique groove of mitrates, orientation with the big-plated side downwards would be implied. Such a homology is most unlikely. The strut does not resemble an intercameral ridge, and was probably a purely mechanical feature (p. 258) that lost its function and disappeared when one face of the animal came to be built of big plates. If the strut were homologous with the oblique ridge there would be no homologue in mitrates for the pharyngo-visceral line.

In summary, therefore, the chambers of the theca of *M. i. miloni* consisted of buccal cavity, left pharyngeal chamber, right pharyngeal chamber, anterior coelom, posterior coelom and left and right atria. In ontogeny the left pharyngeal chamber must have been separate from the anterior coelom from a very early stage. The right pharyngeal chamber certainly, and the posterior coelom probably, arose as outpouchings from the left pharyngeal chamber. The rectum opened into the left atrium as in a tunicate tadpole. Left gill slits probably preceded right gill slits in ontogeny as in amphioxus. In its probable origin from the pharynx, the posterior coelom can be compared with a tunicate epicardium. The oesophagus probably opened into the left pharyngeal chamber near the junction with the right pharyngeal chamber. It was the big-plated side of *M. i. miloni* that was uppermost and corresponded to the dorsal side of a cornute. Finally, the earliest-known mitrocystitid was in some ways transitional, in the arrangement of its chambers as in other respects, between cornute and mitrate conditions.

THE STEM: The posterior stem of *M. i. miloni* consists of about fifteen segments and ends abruptly. Each segment contains a dorsal ossicle (do in Fig. 17b) and paired ventral plates (vp). Successive dorsal ossicles articulate with each other at inter-ossicular articulations (iaf in Fig. 17b) which would have allowed vertical flexing.

The precise mode of imbrication of plates and ossicles is important (Fig. 18). Dorsal to the interossicular articulation the back of each ossicle overlaps the front of the one behind. Similarly, the back of each pair of ventral plates overlaps the front of the pair behind. The lateral, ventral margins of a dorsal ossicle overlap the upper margins of the ventral plates of the same segment. But, certainly in *M. barrandeii* (at x in Pl. 6, figs. 3, 5) and probably in *M. i. miloni* in the uncrushed condition (Pl. 5, fig. 5 at point x), the posterior, upper corners of a ventral pair

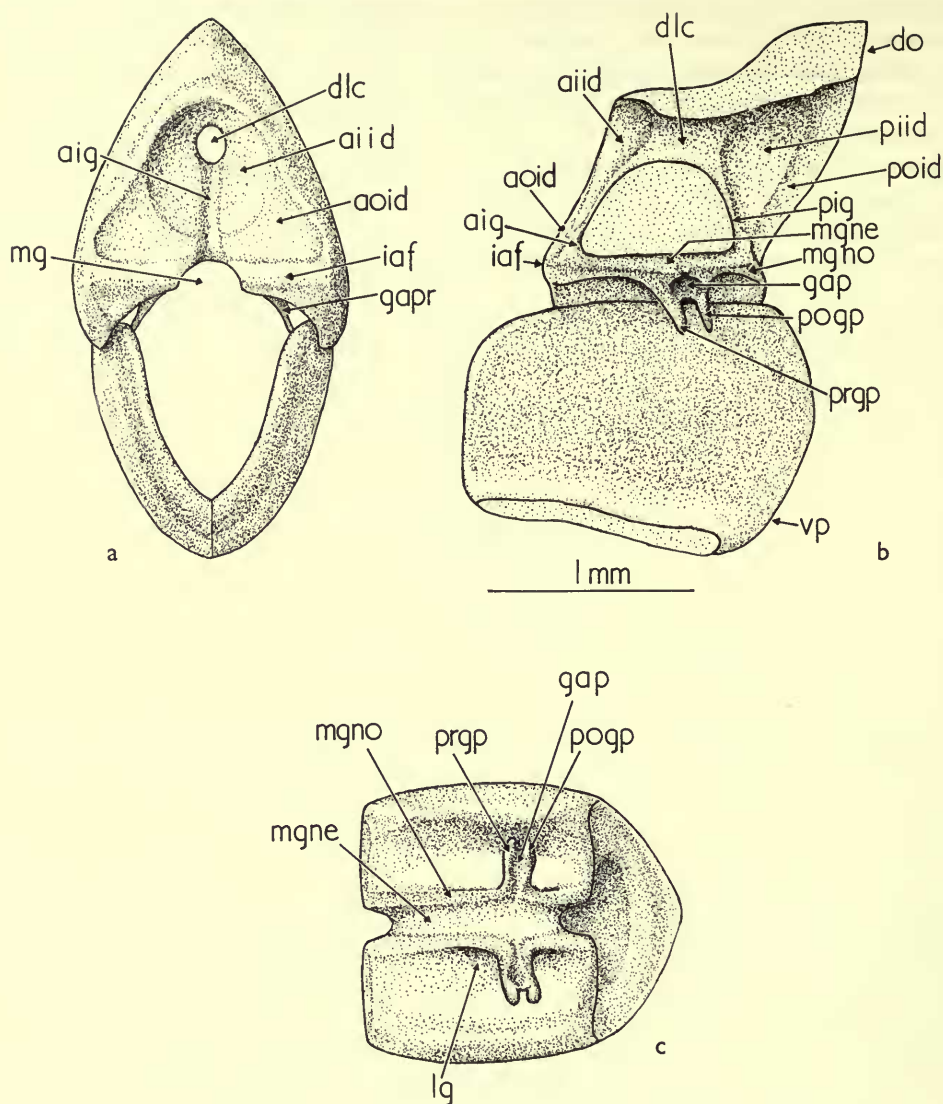


FIG. 17. *M. i. miloni*. Reconstruction of the skeleton of a posterior stem segment. a. anterior aspect; b. sagittal section; c. ventral; d. posterior aspect. aig = anterior ossicular groove; aiid = anterior inner, interossicular depression; dlc = dorsal longitudinal canal; do = dorsal ossicle; gap = ganglionic pit; gapr = ganglionic process; iaf = interossicular articular facet; mg = median groove; mgne = median groove (neural); mgno = median groove (notochordal); pig = posterior interossicular groove; piid = posterior inner interossicular depression; pagp = postganglionic process; poid = posterior outer interossicular depression; prgp = preganglionic process; vp = ventral plate.

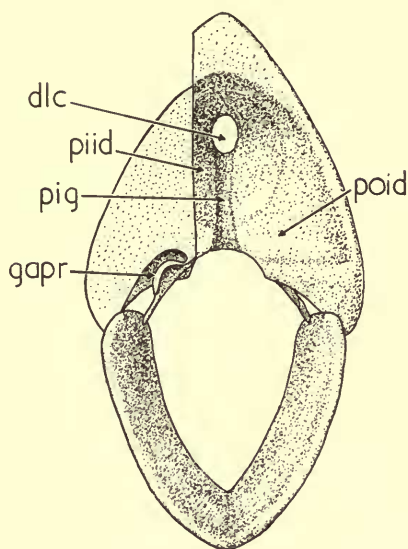


FIG. 17d.

of plates embrace the lower front corners of the next dorsal ossicle behind. A similar imbrication pattern, but with the ventral plates overlapping the dorsal ossicle behind still more extensively, also exists in *Chinianocarpus thoralis* (Ubaghs 1961a, fig. 1E, and personal observation).

According to Prof. Ubaghs' interpretation (1961b) the ventral stem plates of mitrates, which he homologizes with the dorsal stem plates of cornutes, were cover plates capable of opening outwards, and the whole stem was an arm. It is clear that the imbrication just described is very ill-suited to allow the ventral plates to open outwards and, like the detailed stem structure of *Cothurnocystis curvata* (p. 276), argues against Prof. Ubaghs' interpretation. It is also clear that Prof. Ubaghs must be mistaken if, as here maintained, the massive posterior stem ossicles were dorsal in mitrates and ventral in cornutes, for in neither case can the sculpture on their internal surfaces correspond to the *outside* of a water-vascular system.

The internal sculpture of the posterior stem ossicles is very complicated (Fig. 17, 18; Pl. 6, figs. 10, 11; Pl. 7, fig. 5). Above the articulations each ossicle is excavate at back and front, with posterior and anterior, inner and outer depressions (aiid, aoid, piid, poid). Also, in the median plane, there are anterior and posterior inter-ossicular grooves (aig and pig) which connect with a dorsal, longitudinal canal (dlc) perforating the ossicle. On the ventral surface of the more anterior ossicles there is a broad, median groove (mg) which becomes progressively deeper posteriorly in the stem till it passes, in the most posterior ossicles, into a median canal (mc in Pl. 6, fig. 5). In each ossicle the median groove or canal gives rise to paired pits (gap). Each pit is excavated in the ventral surface of a process (gapr) which bifurcates outwards into two prongs (prgp anteriorly and pogp posteriorly). On

each side of the median groove, in the ventral surface of the ossicle, are lateral grooves (lg). Sometimes the lateral grooves are deepest over the processes gap (Fig. 17c; Pl. 6, fig. 5). Sometimes, on the other hand, the lateral grooves are filled with skeleton dorsal to those processes, in which case the natural moulds of the pits on gap are visible dorsally (Pl. 6, fig. 10; Pl. 7, fig. 4).

The structure of the median groove or canal is highly significant. The groove or canal seems to have enclosed two longitudinal soft structures. The first of these was broadly cylindrical and determined the fundamental shape of the groove or canal. It came in actual contact with the parts of the groove marked mgno in Fig. 17b, c. The second structure was thin and strap-like and coated part of the

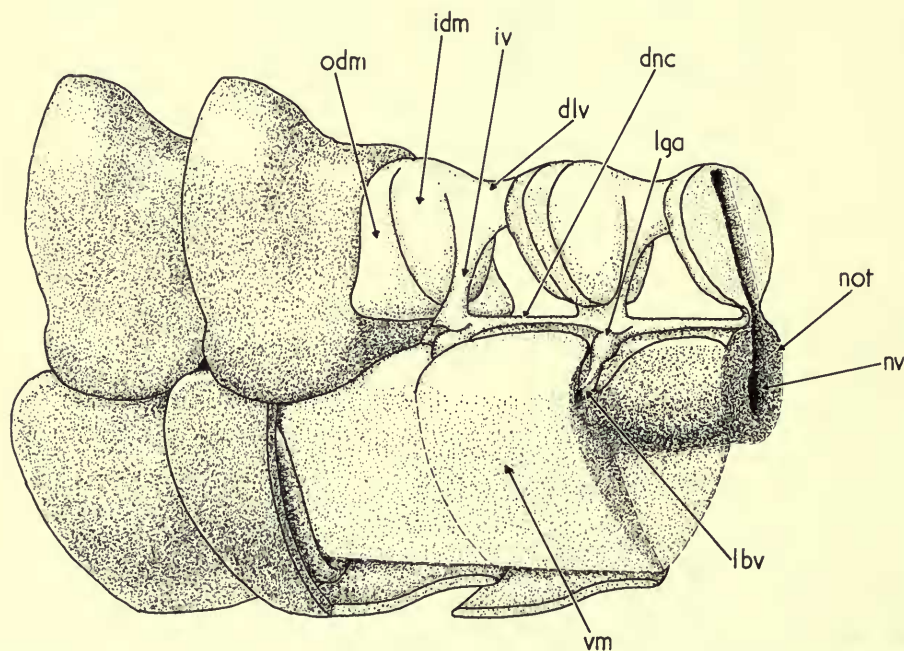


FIG. 18. *M. i. miloni*. Block diagram of posterior stem. dlv = dorsal longitudinal vessel; dnc = dorsal nerve cord; idm = inner dorsal muscle; iv = interossicular vessel; lbv = lateral blood vessel; lga = lateral ganglion; not = notochord; nv = notochordal vessel; odm = outer dorsal muscle; vm = ventral muscle.

dorsal surface of the first structure. It occupied the parts of the groove marked mgne in Fig. 17b, c and sent out lateral projections to the cups of the processes gap. Natural moulds of the median groove, giving a representation in rock of the original soft structures, are shown in Pl. 6, fig. 10 and Pl. 7, fig. 2. The more dorsal structure became narrower, thinner and less evident posteriorly.

As regards interpretation, the broad cylindrical structure in the median groove, by analogy with crinoids, was the chambered organ. Being an anti-compressional structure it was placed at the level of the interossicular articulations, in the principal axis of the stem, which would not shorten or lengthen on bending. Again by analogy

with crinoids, the structure coating the chambered organ would be the peduncular nerve. Its nervous nature is consistent with its strap-like shape and with the way it communicates with the cups of the processes gap (ganglionar processes), for such cups could well contain ganglia. The peduncular nerve of *M. i. miloni* therefore rested on the dorsal surface of the chambered organ, or, in chordate terms, the dorsal nerve cord rested on the dorsal surface of the notochord. It is noteworthy that the dorsal nerve cord rests directly on the notochord in tunicate tadpoles, amphioxus, Agnatha and the embryos of other vertebrates, and also in myxinoids and petromyzontoids it has, as in *M. i. miloni*, a distinctly strap-like shape. The paired segmental ganglia of *M. i. miloni* can be compared with those in the tail of appendicularians (Martini 1909). There is no trace of separate dorsal and ventral spinal nerve roots. The nervous and other soft structures of the posterior stem of *M. i. miloni* are reconstructed in Fig. 18.

Turning now to the musculature, the posterior stem could either flex ventrally or stick out straight, as indicated by the interossicular articulations and imbricating ventral plates. This is confirmed by fossils evidently preserved in the position of death. Pl. 6, figs. 3, 6 (*M. barrandei*); Pl. 7, fig. 5 (*M. incipiens incipiens*) and Pl. 5, fig. 5 (*M. i. miloni*) show straight posterior stems or portions of them. Conversely, Pl. 10, fig. 2 (*M. i. miloni*) shows the stem bent ventrally in the normal position of preservation for the subspecies. Muscles would therefore be needed on at least one side of the articulations, i.e. either dorsally or ventrally, and muscles or ligaments on the other side.

It seems likely that the space between dorsal ossicles and ventral plates was largely filled with muscle. The opposing muscles or ligaments must have been sited in the interossicular depressions. The inner interossicular depressions are very deep and therefore probably contained muscle. The outer interossicular depressions may have contained ligament, or a different sort of muscle. The structure (probably a blood vessel) filling the interossicular grooves probably separated right and left muscle blocks in the interossicular depressions. Repetition of interossicular depressions indicates serial repetition of dorsal muscle blocks.

The ventral muscles were probably also segmented, with the muscle blocks situated between the ganglia. The divisions between muscle blocks are indicated by: 1. the above-mentioned skeletal infilling that sometimes interrupts the lateral grooves dorsal to the ganglionar processes; and 2. the occasional presence of faint ridges on the ventral surface of the ossicle, or grooves in the internal mould, which point downwards and backwards (gmb in Pl. 7, fig. 5) and whose upper ends coincide in position with the ganglia.

The blood system of the posterior stem is difficult to reconstruct. It probably included: 1. a dorsal longitudinal vessel (dlv), occupying the dorsal longitudinal canal; 2. interossicular vessels (iv in Fig. 18), occupying anterior and posterior interossicular grooves; 3. transverse vessels, connected with the sides of the notochord (lbv in Pl. 9, fig. 3) ventral to the segmental ganglia; and 4. a notochordal vessel running down the middle of the notochord.

The evidence that the interossicular grooves carried blood vessels is that: 1. although they emerge from the notochord through the dorsal nerve cord, they seem

to be too wide to have carried only an upward extension of the nerve cord, so far as the thickness of the nerve cord can be judged from the form of the median groove; 2. the dorsal muscles would need a blood supply. In the mitrate *Lagynocystis pyramidalis* interossicular depressions for dorsal muscle and interossicular grooves were present (personal observation) but there was no dorsal longitudinal canal. In this form, therefore, the dorsal muscles must have been supplied with blood up the interossicular grooves. By analogy it is therefore likely that the interossicular grooves of *M. i. miloni* also carried a blood vessel.

The existence of a vessel down the middle of the notochord is not certain, but is suggested by the following pieces of evidence: 1. The crinoids have such a vessel (haemal strand); 2. The interossicular and transverse vessels, which are joined to the notochord, could well have connected with a notochordal vessel. At the least, they indicate extensive vascularization inside the notochord; 3. There was probably no longitudinal vessel ventral to the notochord in *M. i. miloni* since none could have existed in cornutes, and no vessels which could have come directly from a ventral longitudinal vessel are seen to connect with the ventral side of the notochord when this is enclosed by skeleton (Pl. 9, fig. 3); 4. *L. pyramidalis* lacked a dorsal longitudinal vessel. Assuming, for the reasons given under (3), that this form also lacked a ventral longitudinal vessel, then a notochordal vessel must have existed. In such a fundamental feature *M. i. miloni* would probably resemble *L. pyramidalis*.

In summary, the posterior stem of *M. i. miloni* certainly had a notochord, a dorsal nerve cord giving rise to paired, segmental ganglia, and segmentally repeated muscle blocks. The vascular system included a dorsal longitudinal vessel, interossicular vessels that left the notochord through the dorsal nerve cord, transverse vessels, and probably a longitudinal vessel inside the notochord. The dorsal nerve cord resting directly on the notochord is a prime chordate feature. The vascular system, so far as can be worked out, seems to have been more like that of a crinoid.

The medial stem of *M. i. miloni* much resembles two posterior stem segments (std in Fig. 13a) with the dorsal ossicles fused to form what is known as a styloid (Jaekel 1918). The posterior surface of the styloid is very much like that of a normal dorsal ossicle (Pl. 7, fig. 3) with inner and outer, posterior interossicular depressions (piid, poid), interossicular articulations and posterior, interossicular groove (pig). The most obvious difference from a normal dorsal ossicle is that the dorsal longitudinal canal turns sharply upwards anteriorly. The interossicular grooves between the two segments of the styloid fuse to form an interossicular canal (ic) which presumably ran upwards to join the dorsal longitudinal canal. Neither the middle part of the dorsal longitudinal canal of the styloid, nor the dorsal part of the interossicular canal have been seen, however. The anterior surface of the styloid carries a broad lumen (als in Pl. 6, fig. 12), presumably serially homologous with anterior inner and outer interossicular depressions of a posterior stem ossicle. The dorsal longitudinal canal entered this lumen dorsally. A vertical groove (vgls of Pl. 6, fig. 12) posteriorly must be serially homologous with the anterior, interossicular grooves. The lateral grooves (lg) of the styloid produce a serrated internal mould with the deepest parts of the groove dorsal to the seg-

mented ganglia. The median groove differs little from that of the posterior stem ossicles.

The anterior stem is usually poorly preserved but probably contains about ten segments. The skeleton of each segment consists of four plates (left, dorsal and ventral, and right, dorsal and ventral) round a broad lumen. In *M. barrandei* (Pl. 6, figs. 3, 5) the anterior stem could certainly flex upwards so as to lift the posterior stem; this was presumably also possible in *M. i. miloni*. By analogy with *Mitrocystites mitra* (p. 322) the anterior stem of *M. i. miloni* could probably also flex sideways. In order to flex without telescoping, a median, anti-compressional structure would be needed, i.e. a chambered organ or notochord. There must also have been muscles, probably divided into segmental blocks, a dorsal nerve cord, segmental nerves and a longitudinal blood vessel or vessels.

The reason why the massive ossicles of the posterior stem of mitrates were dorsal, whereas those of cornutes were ventral, is almost certainly functional. The posterior stem of cornutes was adapted for flexing upwards and the necessary shortening of the dorsal side was made possible by a series of imbricating plates. The posterior stem of mitrates was adapted for flexing downwards and the imbricating plates are therefore ventral, while the articulations between the massive dorsal ossicles prevented shortening along the principal axis.

Chinianocarpus thorali, as in other features, is transitional in the posterior stem structure from the cornute condition. Like all other mitrates it has an imbricating series of plates ventrally and a series of articulated ossicles dorsally, so that the stem must have been able to flex downwards. However, the ossicles are relatively less massive than in *M. i. miloni* and *Mitrocystites mitra*, and the ventral plates relatively larger. Also, in the only two specimens of *C. thorali* where the posterior stem is known (personal observation and Ubaghs 1961a, Fig. 1D, E) the posterior stem definitely curves gently upwards.

The actual transition between cornutes and mitrates must have had neither styloid nor stylocone, but simply two segments like those of the posterior stem, articulated with each other so that they could bend either up or down. The re-development of a solid element in the medial stem, preventing the anterior stem muscles from pulling against the posterior ones, would be highly advantageous.

THE BRAIN AND CRANIAL NERVES: The brain and cranial nerves of *M. i. miloni* can be reconstructed in detail (Fig. 19a, b, c) partly because they were extensively enclosed by skeleton, and partly because, when nerves ran in soft-tissue-filled spaces in the skeleton, their exact positions can often be determined. Thus, in the posterior ventral skeleton, the nerves ran in an extensive, median, soft layer (Fig. 15F, G, H, I), presumably consisting of connective tissue, between a thin inner and a thick outer layer of calcite. The positions of the nerves are indicated by dilatations of the soft layer. These dilatations are flanked by flat-topped thickenings of the outer layer (tol in Pl. 5, fig. 8), and often roofed over by gentle folds in the inner layer (as in Pl. 5, fig. 11). The inner layer of calcite is absent from the median and anterior, more flexible parts of the ventral skeleton, and the connective tissue layer, if it existed in this region, cannot be recognized.

Upward extensions from the median layer of the ventral skeleton entered the

dorsal skeleton near the posterior right and left corners of the theca (Fig. 15I) and there remained separate from the thecal cavity because of an inner layer of calcite. More anteriorly and laterally other extensions from the median soft layer of the ventral skeleton touched the inner face of the dorsal skeleton which was excavated to receive them (Fig. 15F, G, H; sl in Pl. 7, fig. 6), but these extensions were not separated from the thecal cavity by an inner layer of calcite.

In addition to these direct upward extensions of the ventral median layer, the dorsal skeleton contained an extensive irregular system of spaces in the calcite. These spaces must have been filled with soft tissue and are particularly evident across sutures (e.g. sl in Pl. 6, fig. 7).

The histological origin of the soft-tissue-filled spaces could not be studied, in the absence of material showing actual stereom mesh. Resorption of calcite may have played a part in their origin, but of this there is no proof. The presence of casts of a calcite cleavage network (ccc in Pl. 5, fig. 2; Pl. 6, fig. 7) is the only direct indication that the hard skeleton was calcite.

The nervous nature of the structures here called nerves, which was already recognised by their discoverer Chauvel (1941), is virtually certain because: 1. like the aboral nerves of crinoids they radiate from the region where the stem joins the theca; and 2. they often had a very compressed cross section (Fig. 15F, G; Pl. 5, figs. 6, 8, 11).

The brain, as in cornutes, was lodged in the theca, just in front of the stem. The encephalic mould is divided into anterior (ap), medial (mp) and posterior (pp) parts (Fig. 19a-c; Pl. 6, figs. 1, 4). The anterior part is frond-shaped and developed along the posterior, median, dorsal suture (M_{1LD}/M_{1RD}). The medial and posterior parts, like the brain of cornutes, lie in a cerebral depression which, however, is excavated in the dorsal instead of the ventral first marginals, i.e. M_{1L} and RD instead of M_{1L} and RV . The side walls of the posterior part of the cerebral depression received the most anterior plates of the stem. The medial part of the encephalic cast is bounded ventrally by two hypocerebral processes (enclosing lmp in Pl. 6, fig. 2—*M. barrandei*) which almost, but not quite, meet at the mid-line. Above these, the middle part of the encephalic cast communicates with the thecal cavity by a medial part foramen (mpf in Pl. 6, fig. 4 and Pl. 6, fig. 2—*M. barrandei*) through which, by analogy with *Mitrocystites mitra* (p. 322), passed paired medial part nerves (mpn). Ventral to the hypocerebral processes the thecal cavity communicates with the lumen of the anterior stem. In *M. barrandei* (Pl. 6, fig. 2) and

FIG. 19. *M. i. miloni*. Reconstruction of brain and cranial nerves. a. dorsal aspect; b. anterior aspect of posterior part; c. right aspect of left side. af = anterior furcation of palmate complex; ap = anterior part of brain; bc = buccal cavity; csb = carrot-shaped body (lateral-line ganglion); csbn = nerve to carrot-shaped body (nerve to lateral-line ganglion); e = vestigial eye; mp = medial part of brain; mpn = medial part nerves (bases of optic nerves); n_0 = nerves emerging from posterior coelom near midline; n_1 to n_8 = nerves of palmate complexes; olo = olfactory openings; pal = palmar nerve; pb = pyriform body; pc = peripheral canal; pf = posterior furcation of palmate complex; pp = posterior part of brain; ppn = posterior part nerve; r = rectum.

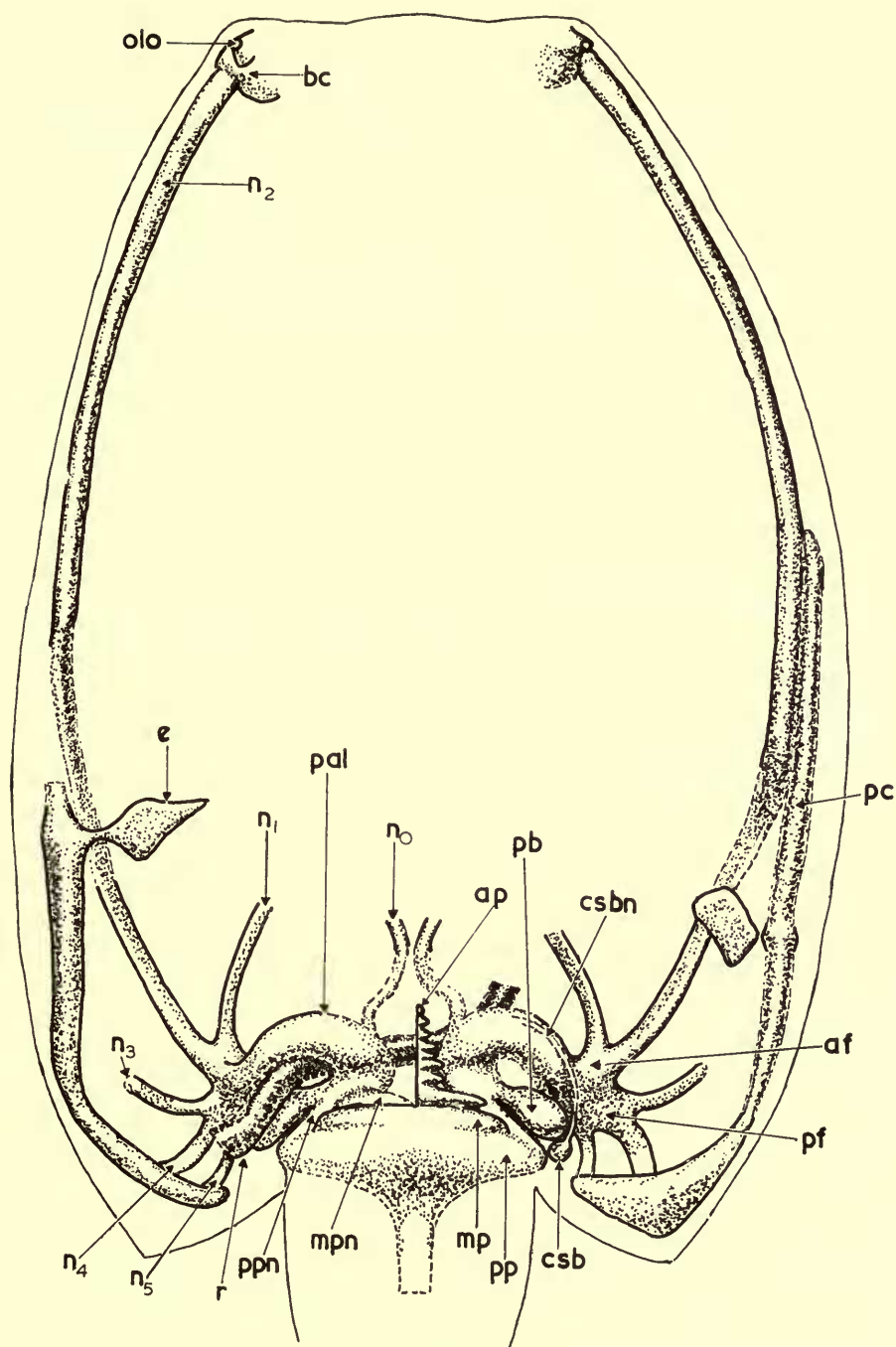


FIG. 19.

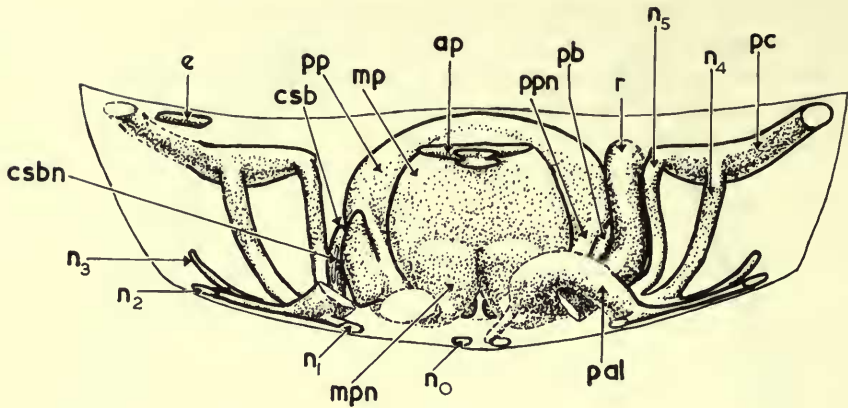


FIG. 19b.

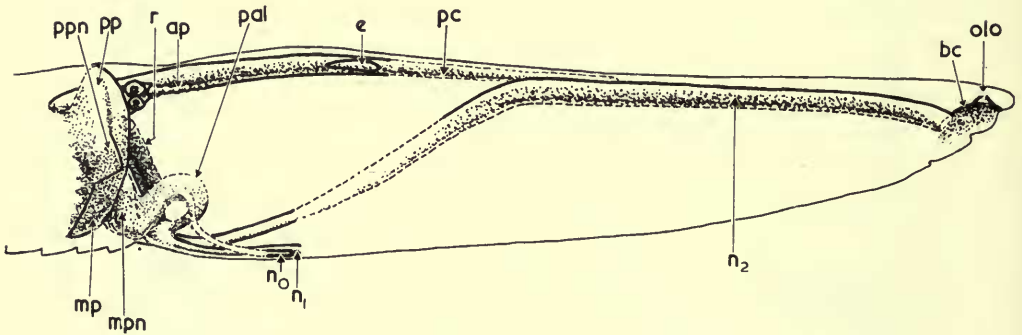


FIG. 19c.

Mitrocystites mitra (Pl. 9, fig. 6) the part of the encephalic cast enclosed by the hypocerebral processes is slightly swollen, so that a lower and an upper part of the medial brain (lmp, ump) can be distinguished. There are paired structures on the front of the posterior part of the encephalic cast, running towards the median plane and downwards (posterior part nerves, ppn in Pl. 6, figs. 2, 4).

The main structures related to the cranial nerves are as follows:

1. Right and left palmate complexes, so called because each consists of a trunk and five digitations. The proximal trunks (palmar nerve, pal in Fig. 19a-c; Pl. 5, figs. 6, 8; Pl. 7, fig. 1) first show themselves where they touched the anterior wall of the posterior coelom (Pl. 7, fig. 1) and, for some reason, caused the wall to calcify. The palmar nerves then entered the soft layer of the ventral skeleton at the ventral, anterior corners of the posterior coelom. After a short distance they divided into anterior and posterior furcations (af, pf in Fig. 19a-c; Pl. 5, figs. 6, 8). Each anterior furcation gave rise to two nerves (n_1 , n_2) and each posterior

furcation to three nerves (n_3 , n_4 , n_5). The courses of these will be described when their nature is considered (p. 305). The left palmar nerve (Fig. 19c), judging by the trace that it left in the front wall of the posterior coelom, looped over the rectum before entering the ventral skeleton.

2. Right and left peripheral canals (pc in Fig. 19a-c; Pl. 5, figs. 3, 6; Pl. 6, fig. 7). These were spaces in the dorsal skeleton which were well developed on either side posteriorly and the right one can be traced at least as far forward as the suture $M_{3/4R}$. Both canals probably ended shortly in front of this. Posteriorly they they received nerves n_4 and n_5 of the palmate complexes.

3. Right and left "pyriform bodies" (pb in Fig. 19a, b; Pl. 5, fig. 6; Pl. 6, fig. 4; Pl. 9, fig. 1; Pl. 10, fig. 3) homologous with those of cornutes. These bodies lay as if pressed against the front faces of the posterior part nerves, but were actually separated from these by a thin layer of skeleton. They were totally enclosed in cupules in M_{ILD} and v and M_{IRD} and v , except for a slit-like opening on the median side of each body.

4. A "carrot-shaped body" (csb in Fig. 19a, b; Pl. 5, fig. 6; Pl. 9, fig. 4; Pl. 10, fig. 3) just behind the right pyriform body. This underlay and communicated with the narrow groove (ng) on the surface of M_{IRV} . It received a laterally compressed nerve anteriorly (csbn in Pl. 10, fig. 3).

5. Right and left conical openings into the buccal cavity (olo in Fig. 19a, c; Pl. 5, figs. 7, 9).

6. Right and left nerves (n_6) that entered the soft layer of the ventral skeleton from the posterior coelom, near the mid-line (Pl. 5, fig. 11), within the plate V_{PM} .

It is interesting to compare the brain and cranial nerves of *M. i. miloni* with those of cephalaspids (Figs. 20, 21), for the latter are the only early Agnatha where these organs are known in detail. There is broad agreement that the brains of these fish much resembled that of *Petromyzon*, but there is unfortunately much difference of opinion as regards the cranial nerves.

The classical hypothesis of head segmentation has caused these differences of opinion, and therefore demands a digression. The version of the hypothesis expounded by Goodrich (1918, 1930) has been particularly influential (see e.g. de Beer 1937: 15 ff.; Young 1950: 144 ff.) and can suitably be explained here. According to Goodrich the branchial slits originally emerged between somites serially homologous with those of the trunk. Also there were "premandibular" and "mandibular" pairs of gill slits anterior to any now remaining, i.e. anterior to the spiracles of gnathostomes or to the homologous first branchial slits of Agnatha. Between the "mandibular" and "premandibular" pairs of gill slits lay the first prootic or "premandibular" pair of somites. These were associated with the trabeculae cranii, which represented the skeleton of an original "premandibular" branchial arch. Between the "mandibular" and the spiracular pairs of gill slits lay the second prootic or "mandibular" pair of somites, with which the mandibular skeleton was associated—originally as a gill arch, little different from the arches behind it. Between the spiracular and the first post-hyoidean gill slits lay the paired spiracular somites associated with the hyoid arch. The innervation of all interbranchial somites was supposed originally to have been like that of the trunk

somites, with paired dorsal and ventral roots. The dorsal roots, however, would have had a strong branchial component. Accordingly, the first prootic ("pre-mandibular") somites would have had the paired profundus branches of the trigeminal as their dorsal-root, branchial nerves, and would have had the oculo-motor nerves as their ventral roots. The second pair of prootic ("mandibular") somites would have had the rest of the trigeminal complex as their dorsal-root, branchial nerves, and the trochlear nerves as their ventral roots. The third pair of prootic somites would have had the facial nerves as their dorsal-root, branchial nerves and the abducens nerves as their ventral roots. The hypothetical ventral roots and paired somites associated with the first post-hyoidean arch have supposedly disappeared, but the glossopharyngeal nerves would have been the corresponding dorsal-root, branchial nerves. Each of the dorsal-root nerves going to the first few pairs of metotic somites supposedly had originally a branchial branch to the "corresponding" gill slit, but these branchial branches have since bunched together to form the paired vagus nerves. Consequently each metotic somite now has a ventral and dorsal spinal root nerve and is also, in theory, related to a branchial branch of the vagus. More detailed expositions of the hypothesis can be found in the cited works of Goodrich, de Beer and Young.

In considering this hypothesis, it must first be emphasized that branchiomerism and trunk segmentation are, of course, real phenomena. It is their supposed, original, simple relationship which is in doubt, and which has not everywhere been accepted (e.g. Romer 1949 : 555). Again, it is likely that the mandibular arch represents an original branchial arch, serially homologous with those behind it (e.g. Devillers 1958 : 573) and it is certain that the mandibular and maxillary branches of the trigeminal nerves were the original innervation of the mandibular and maxillary skeleton. It is very doubtful, however, that mandibular and pre-mandibular gill slits ever existed, or that the trigeminal complex was originally branchial. Finally, the prootic somites are real entities which give rise to the oculo-motor muscles, and they are really innervated by the oculo-motor, trochlear and abducens nerves. But the serial homology of the prootic somites with the metotic somites or with the mesodermal pouches between the gill slits, the grouping of their nerves as ventral roots corresponding to dorsal roots represented by profundus, "true" trigeminal and facial nerves, and the separation of the prootic somites by hypothetical gill slits, are all baseless suppositions.

The arguments against the segmentation hypothesis in general, and Goodrich's version of it in particular, were forcefully marshalled by Kingsbury (1926). His case can be summarized as follows:

1. Gill slits seldom equal in number, and always appear later than and ventral to, the divisions between the trunk somites of the same region, and in amphioxus the gill slits do not even appear simultaneously on right and left sides. It may be added that there is certainly no serial relationship whatever between gill slits and trunk (i.e. tail) musculature in tunicate tadpoles.

2. The prootic somites differentiate, in general, from behind forwards, whereas the metotic somites, their supposed serial homologues, differentiate from in front backwards.

3. The nerves innervating the prootic somites, in particular the trochlear and abducens, do not have the central relations expected for somatic motor nerves, and do not pair with the profundus, "true" trigeminal and facial nerves as the hypothesis would require. The trochlear, in particular, always comes off the brain dorsally, after decussation of fibres.

4. The trigeminal nerves do not innervate gill slits in any living vertebrate.

5. The vagus nerve is never seen to be related to the spinal nerves in the way that the hypothesis suggests is primitive. In addition, the intestinal branch of the vagus will not fit into any segmental scheme. It may be added that the oldest-known vagus nerves—those of cephalaspids—are similar in morphology to the vagus nerves of living fish and agnathans.

Among recent works that adopt a segmentationist viewpoint, the contributions of Jarvik (1954 : 71 ff.), Bertmar (1959, esp. p. 341 ff.), Stensiö (1963, esp. p. 29 ff.) and Tarlo & Whiting (1965) should be mentioned. It is fair to say that all these authors, convinced that a segmentation scheme of Goodrich type was primitive, have tried to make the structures that they saw fit into it. The results are fairly plausible but not convincing enough to prove the truth of the scheme.

Jarvik, with great plausibility, serially homologised the elements of the mandibular arch in the crossopterygian *Eusthenopteron* with the elements of the hyoid arch and post-hyoidean arches behind. He also tried to recognise, but far less convincingly, the skeletal elements of a premandibular arch, anterior to the mandibular arch. Bertmar tried to do the same for certain Recent teleostean fishes. The account given by Jarvik (1954 : 71) of the views of previous workers is most revealing. For when authors such as Holmgren, Jarvik, Jaekel, Severtsoff and Allis, to name only some, disagree so completely, even as to the number of arches, it seems doubtful if such arches exist.

Stensiö (1963, esp. p. 29 ff.) elaborated the classical subdivision of the trigeminal complex, and wrote of paired trigeminal I and paired trigeminal II which he held to innervate mandibular and premandibular arches. Both pairs of trigeminals were supposedly provided, in cephalaspids, with dorsal sensory and ventral branchial branches. However, Stensiö gave no evidence of the existence of the paired dorsal branches of trigeminal II in cephalaspids (1963 : 29). Further, the interpretation of the other trigeminal branches (profundus, maxillary and mandibular), which careful reading shows to be identical to the interpretation of Wängsjö (1952), is not the most natural that can be offered.

Tarlo & Whiting (1965) reinterpreted certain paired pits inside the head shield of Cyathaspididae (Heterostraci). They saw in them indications of a complete series of head somites where previous authors had found indications of gill chambers. They also regarded the first two pairs of the pits that they figured as showing the positions of prootic somites. It is worth noting that Denison (1964 : 344) has, on good grounds, denied the existence of the first of these pairs of pits. Central to the argument of Tarlo & Whiting is the fact that the pits are sometimes striated approximately transverse to their axes, i.e. sub-parallel to the long axis of the animal. The authors therefore suggested that the striations cannot represent gill lamellae as Stensiö had suggested (1958 : 366) but must somehow be related

to somites with fibres running parallel to the long axis of the animal. It is true that gill lamellae cannot be transverse to the direction of flow of water through a gill, but it is by no means obvious that the striations would be transverse to the direction of flow in Cyathaspididae, if the pits were occupied by gill pouches. Incidentally, the skeleton surrounding the gill chambers of Cephalaspididae shows very similar striations (see e.g. Stensiö 1958 : 197, fig. 115; 1963 : 33, fig. 16; Wängsjö 1952 : 159, fig. 15B). These also are roughly, though not accurately, transverse to the length of the gill chambers, but are nevertheless parallel to the likely direction of flow of water through the pharynx. In any case the distribution of the striations in cephalaspids, beginning just behind the peripharyngeal bands (Wängsjö, *loc. cit.*), shows that, whether or not they represent gill lamellae, they

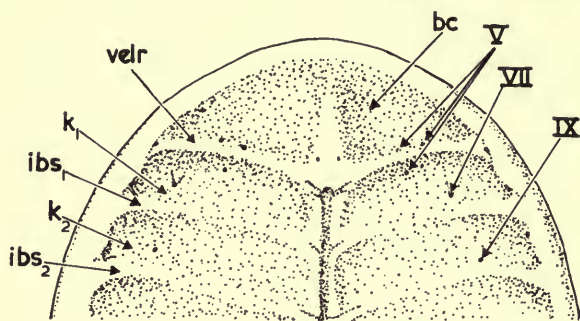


FIG. 20. Anterior part of roof of oralo-branchial chamber of the cephalaspid *Nectaspis areolata* Wängsjö. Redrawn after Wängsjö (1952, fig. 15c), relabelled. bc = buccal cavity; ibs_{1, 2} = interbranchial septum; k_{1, 2} = branchial pouches; velr = velar ridge; V, VII, IX trigeminal, facial and glossopharyngeal nerves.

must certainly show the positions of gills. It is likely that they had the same significance in cyathaspidids. If interpreted as housing gill chambers, the first pairs of pits that exist (the second pair of Tarlo & Whiting) is not so far forward that it could not be homologous with the spiracular chambers of gnathostomes or the first gill chambers of Agnatha. Also, even if the pits housed interbranchial mesodermal pouches, as Tarlo & Whiting suggest, there is no sign that these pouches would form a continuous series with the trunk somites. The pits always cease just anterior to the branchial openings, and therefore well anterior to the back of the head shield (Denison 1964 : 345).

Regarding cephalaspid cranial anatomy, there is a large oralo-branchial chamber in the head shield (Fig. 20) which is divided into a right and left series of smaller chambers. Stensiö (1927, 1958, 1963) maintained that all these smaller chambers carried branchial chambers. He also maintained (1927 : 167) that the division between the first and second chambers may have carried the velum, so that the first supposed pair of gill slits would be actually in front of the velum and would comprise perforations in the wall of the stomodeum. According to Stensiö the buccal cavity would correspond only to a small area at the extreme front end of the oralo-branchial cavity (dpr in e.g. Stensiö 1927, fig. 36). Wängsjö (1952, esp.

pp. 154 ff.), on the other hand, contended that the first pair of chambers (bc in Fig. 20) represented the buccal cavity, that the ridge behind it (velr in Fig. 20) supported the velum, as Stensiö had thought, and that only the chambers behind this ridge (k_1 , k_2 in Fig. 20) were branchial. This second view is almost certainly correct. The chambers making up the first pair are clearly different from the chambers behind them (cf. Fig. 20, and e.g. Wängsjö 1952, fig. 15a, b, c). They lie in front of the distinct median groove in the roof of the oralo-branchial chamber made by the dorsal aorta. They never have the above-mentioned transverse striations which sometimes occur on the other chambers, and which probably indicate gills, and they never have any sign of branchial openings. Wängsjö (1952 : 135) described grooves in the skeleton for peripharyngeal bands, within the second pair of chambers, and the striations that indicate gills only occur behind these peripharyngeal grooves. This is exactly parallel to the situation in tunicates, amphioxus and ammocoete larvae. Further, Stensiö's belief in gills anterior to the velum is surprising from both hydrodynamic and comparative points of view, since the velum functions basically as a valve upstream of the gill slits and never has branchial slits anterior to it in any living chordate.

Stensiö (1927, 1958) originally maintained that the first pair of chambers (i.e. what is here interpreted as buccal cavity, bc in Fig. 20) received the right and left profundus branches of the trigeminal, which were thus branchial nerves. The second pair (k_1 in Fig. 20) received the "true" trigeminal nerves—also branchial. The third pair (k_2) received the facial nerves, the fourth (k_3) received the glosso-pharyngeal nerves, and fifth and succeeding chambers received successive branches of the vagus. His views, therefore, tallied well with classical segmentation theory.

Allis (1931) and Wängsjö (1952 : 63) disagreed with Stensiö's original views. They proposed instead that the profundus nerves were weakly developed and ran up through the orbits to the dorsal side of the head. Allis and Wängsjö held further that the nerves to the first pair of chambers (i.e. buccal cavity) were the maxillary branches of the trigeminal and the nerves to the second pair of chambers (i.e. first branchial chambers) were the mandibular branches of the trigeminal. In support of this latter contention Wängsjö cited the absence of swellings that might represent ganglia in the courses of these nerves to the first branchial chambers, which supposedly showed that they were motor nerves like the mandibular trigeminal nerves, but this argument is weak. Ganglia do not always show as obvious swellings of the nerves (cf. e.g. the reconstruction of the cranial nerves of *Petromyzon* by Johnston (1905, Pl. 5) especially the proximal, ganglionar part of the facial nerve) and still less as swellings in the nerve canals. As regards the nerves to more posterior pairs of chambers, Allis and Wängsjö agreed with Stensiö (1927). As already mentioned, Stensiö (1963 : 31) appears to have adopted Wängsjö's interpretation of the nerves to the first two pairs of chambers and of the profundus nerves.

A much more natural interpretation, however, was proposed by Lindström (1949 : 445). His interpretation of the profundus nerves agrees with that of Allis, Wängsjö and Stensiö (1963), i.e. he thought that they were weak, and innervated part of the dorsal surface of the head. For him, however, the paired nerves to the

buccal cavity correspond to the whole of the rest of the trigeminal complex, since this supplies the mouth region in living agnathans and fish. The nerves to the first pair of branchial chambers were the facial nerves, for these supply the first pair of branchial chambers of living agnathans and the homologous spiracles of gnathostomatous fish. The nerves to the second pair of branchial chambers were therefore the glossopharyngeal nerves, and the nerves to the third and succeeding pairs of chambers were the branchial branches of the vagus. Lindström held that

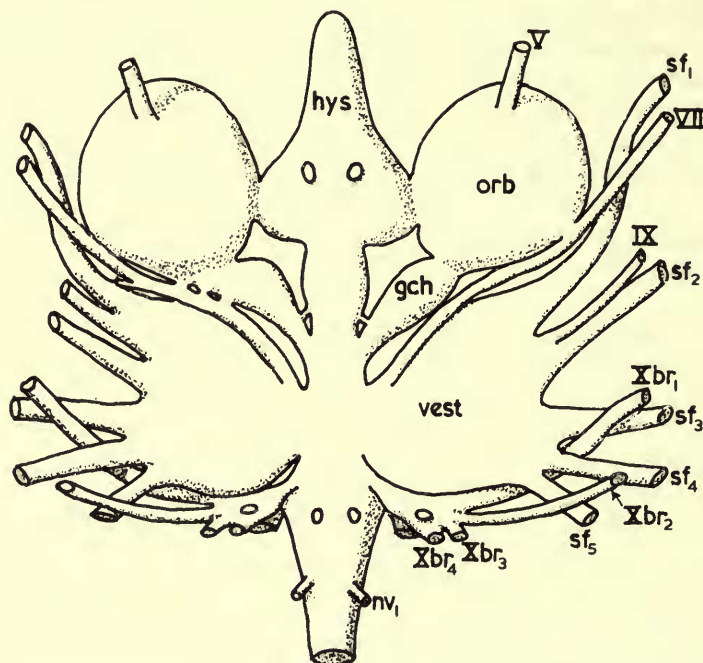


FIG. 21. Ventral aspect of canals associated with brain and cranial nerves of the cephalaspid *Nectaspis areolata* Wängsjö. Ventral aspect, redrawn after Wängsjö (1952, fig. 12), relabelled. gch = trigemino-lateralis chamber; hys = hyphophysis; orb = orbit; sf = sensory field canals; vest = vestibule; V = trigeminal, VII = facial, Xbr₁₋₄ = branchial branches of vagus.

the facial nerves left the brain anterior to the ear and ran through paired canals, the proximal parts of which were labelled I by Stensiö (1927: 136, fig. 28). These canals touched the orbits in parts of their courses (cf. Fig. 21). The glossopharyngeal, according to Lindström, left the brain just behind the ear through the paired canals VIIIp of Stensiö (1927, fig. 28), and ran through the vestibule on their way to the second branchial chambers. Although, therefore, the points of origin and the end organs of the facial and glossopharyngeal were the same as in modern analogues, the intermediate courses of these nerves were somewhat different. Lindström, however, points out that this is not surprising, since the most anterior

gill chambers of cephalaspids lay far forward relative to the brain, compared with modern analogues. There is, indeed, every reason to accept Lindström's interpretation which has been followed in labelling (Figs. 20 and 21).

Other points have been at issue in cephalaspid cranial anatomy. Thus the large paired chambers just behind the orbit (gch in Fig. 21) were regarded by Stensiö (1927) as myodomes for oculo-motor muscles. Wängsjö (1952 : 67 ff.) has shown that sometimes they are fusiform in shape and cannot therefore be myodomes. He identified them as chambers for the trigemino-profundus and anterior lateralis ganglia, and there seems little doubt that he was right.

Again, the well-known dorsal and lateral fields of cephalaspids were regarded as electric fields by Stensiö (1927), but Bohlin (1941), Westoll (1945) and Wängsjö (1952 : 192) thought they were sensory, largely on account of their thinness. They connected the fields, with some doubt, to the lateralis system. Watson (1954 : 20 ff.) elaborated a somewhat similar interpretation, pointing out that the so-called nerve canals (sf₁₋₅ in Fig. 21) to the dorsal and lateral fields were much too wide to have carried only nerves. He suggested instead that they carried canals from the labyrinth and that the whole apparatus was a development of the ear that substituted functionally for the deficient lateralis system. Stensiö (1963 : 38) accepted that the fields in question were sensory fields of a special nature.

The brain and cranial nerves of *M. i. miloni* will now be compared with those of agnathans in general and cephalaspids in particular, assuming that the interpretations of the latter shown in Fig. 20 and 21 are correct.

The brain (Figs. 19a-c) resembles that of a lamprey or cephalaspid, except for being much shorter. The posterior part (pp) corresponds to the medulla oblongata plus the ventral part of the mesencephalon. The posterior part nerves (ppn) are the medullary nerves, presumably including equivalents of everything from trigeminal V to vagus X. Oculo-motor nerves (III, IV, VI) would not be represented as such, for there could be no oculo-motor muscles (cf. *Mitrocystites mitra* p. 319).

The medial part of the brain represents the optic lobes dorsally and the diencephalon more ventrally. The foramen (mpf) would be the outlet for the optic nerves (mpn). The whole of the medial part of the brain dorsal to the optic nerves would be optic in function. The part of the medial part of the brain just ventral and posterior to the optic nerves would, on vertebrate analogies, be functionally related to the hypophysis, which would have lain just beneath the gap between left and right hypocerebral processes. This lower medial part of the brain (lmp), in agreement with its different function, is differentiated from the optic, upper medial part (ump), as mentioned above, by being slightly protuberant in *Mitrocystella barrandei* and *Mitrocystites mitra*.

The anterior part of the brain (ap), which connected with the rest of the brain just dorsal to the optic nerves, would represent the telencephalon, with an olfactory function.

Turning to the palmate complexes, the anterior furcation (af) of each gave rise to n₁ and n₂ (Figs. 19a-c; Pl. 5, figs. 6, 8, 11). The courses of these within the median layer of the ventral skeleton, through most of M_{IL} and R_V, are flanked by

thickenings of the outer calcite layer (see especially Pl. 5, fig. 8). These thickenings suddenly stop anteriorly, but the nerves must clearly have continued beyond them. The nerves n_1 presumably ran forward and innervated the muscles inside the flexible ventral skeleton. The nerves n_2 presumably followed the lateral extensions of the soft layer out of the ventral skeleton (Fig. 15E, F) and can be traced again, after only a short interval, by means of right and left grooves in the skeleton corresponding to a ridge each side of the internal cast (n_2 in Pl. 5, fig. 1). The ridges run forwards into the buccal cavity (n_2 entering bc in Pl. 5, figs. 7, 9).

The nerves n_2 therefore compare at first sight with the nerves that innervate the buccal cavity of cephalaspids, i.e. the right and left trigeminal V, but further consideration refines this comparison. Thus Lindström has shown (1949 : 354, 384, 439) that the trigeminal complex of modern agnatha has paired maxillary and mandibular branches. The same may also have been true of cephalaspids, though direct evidence would not be expected since the relevant parts of the anatomy would be ventral to the dorsal shield. By comparison, therefore, it seems likely that the nerves n_1 of *M. i. miloni* correspond to the mandibular, and n_2 only to the maxillary branches of the trigeminal. The probable motor function of the nerves n_1 agrees with this supposition. The fact that the nerves n_2 innervated the ventral wall of the theca and the lower lip in *Mitrocystites mitra* (p. 322), and probably did so in *M. i. miloni*, does not argue against comparing them with the maxillary trigeminal nerves of cyclostomes, which behave similarly (Lindström 1949 : 439).

The posterior furcations of the palmar nerves (pf in Fig. 19a, Pl. 5, figs. 6, 8) gave rise to nerves n_3 , n_4 and n_5 on each side. The positions of n_3 are defined on each side in the median soft layer of M_{1L} and R_V by thickenings of the outer calcite layer. Their courses cannot be traced in the soft layer after the latter leaves the ventral skeleton. The nerves n_3 of *M. i. miloni* clearly correspond to n_3 of *Mitrocystites mitra* (p. 322), for in both species they lay between the nerves n_2 and the branchial openings. The nerves n_3 of *M. mitra* were clearly optic nerves leading to eyes resting on the sutures $M_{2/3R}$ and L and n_3 of *M. i. miloni* must be vestigial optic nerves. In many specimens of *M. i. miloni* the soft-tissue filled cavities of the dorsal skeleton flanking the sutures $M_{2/3L}$ and R show angular extensions (e in Fig. 19a-c; Pl. 5, fig. 3; Pl. 6, fig. 1) in much the same position as the eyes of *M. mitra*. These extensions may represent vestigial eyes.

Nerves n_4 and n_5 from the posterior furcations (Fig. 19a-c; Pl. 5, figs. 6, 8) can be followed through the median layer of M_{1L} and R_V and into the posterior, dorsal extensions of this layer in M_{1L} and R_D where, ultimately, they join the peripheral canals (pc in Figs. 19a-c; Pl. 5, figs. 3, 6; Pl. 6, figs. 1, 7). In both ventral and dorsal skeleton, their courses are flanked by thickenings of the outer layer of calcite. Nerves n_4 and n_5 are on each side median and posterior to the gill opening and cannot therefore be homologous with any part of the trigeminal complex of an agnathan or fish.

The peripheral canals, judging by their superficial position, were probably sensory, and n_4 and n_5 represent their nerve supply. It is possible that the peripheral canals are homologous to the sensory fields of cephalaspids, but equally possible

that any resemblance is convergent. The possible homology would be inconsistent with the above-mentioned suggestions of Bohlin (1941), Westoll (1945) and Wängsjö (1942 : 1952) that the sensory fields of cephalaspids might be related to the lateralis system, since in *M. i. incipiens* the lateralis system exists in a very primitive form: (see below) and is not related to the peripheral canals. It would also be inconsistent with Watson's (1954) interpretation of these fields as elaborations of the ears, since the lateralis system of *M. i. miloni* was too primitive to include ears.

The palmar nerves, to judge by what comes off them peripherally, must have formed proximally by fusion of medullary nerves (posterior part nerves) and optic nerves (medial part nerves). This is reasonable since in *M. i. miloni*, *M. barrandei* and *Mitrocystites mitra* the posterior part nerves ran forwards, downwards and admedian, and in *M. mitra* direct evidence shows that the medial part nerves ran forwards, downwards and away from the median plane. They could, therefore, easily have fused shortly after leaving the dorsal skeleton.

The nature of the pyriform bodies, the carrot-shaped body behind the right pyriform body, and the narrow groove (ng) in M_{1RV} must be considered together. The pyriform bodies are reminiscent of the trigemino-lateralis chambers of cephalaspids (gch in Fig. 21) in position and their shape suggests that they carried ganglia. As mentioned above, however, Wängsjö (1952 : 67) has shown that the trigemino-lateralis chambers in cephalaspids carried both the trigemino-profundus and anterior lateralis ganglia. Bearing this in mind, it seems likely that the pyriform bodies correspond to trigemino-profundus ganglia alone, that the carrot-shaped body was a lateralis ganglion, that the groove that it underlay was the lateral line and that the canal emerging from the front of the body (csbn) carried a lateral-line nerve.

Several considerations support this view. Firstly, the right and left trigemino-profundus ganglia of *Petromyzon* lie just in front of the anterior lateralis ganglia, just as the right pyriform body lies just in front of the carrot-shaped body. Secondly, lateral-line ganglia are often peripheral in position. And thirdly, Pumphrey (1950) has shown that the acustico-lateralis system, on physiological grounds, must first have appeared as lateral-line.

As regards functioning, the groove (ng) of *M. i. miloni*, because of its position, would often be buried in mud, but this would not affect its efficiency as lateral-line, since the damping effect of half a centimetre of mud would be negligible. Pumphrey has shown (1950 : 7) that the great length of the lateral line in fish makes it possible to locate the position of sound sources. It is therefore interesting that in *Chiniano-carpos thoralis* the groove (ng) is represented only by a pit (personal observation) so that the system increased in length during the evolution of the Mitrocystitidae.

Comparison of the olfactory nerves and telencephalon with cephalaspids is of little help, since the olfactory opening of these fish lay on top of the head between the eyes. This is a highly unusual feature among vertebrates and corresponds to nothing in the mitrocystitids. A more helpful comparison is with Heterostraci. It is generally accepted that a right and left nasal sac opened downwards into the buccal cavity in these fish. Stensiö (1958) opposed this view, but Heintz (1962) argued convincingly in favour of it and refuted Stensiö's reconstructions.

It seems likely that the apices of the conical pits (olo) that open into the buccal cavity in *M. i. miloni* represent the points where the olfactory nerves entered the skeleton. The conical pits may themselves represent the nasal sacs of Heterostraci, but it is perhaps more likely that olfactory sensitivity was distributed over the whole dorsal wall of the buccal cavity, and the conical pits were simply the places where olfactory fibres converged before entering the skeleton.

The cavity containing the anterior part of the brain (ap) had numerous conical extensions to right and left. These extensions probably represent the places where olfactory fibres, or bundles of fibres, left the skeleton. The course of these fibres between the olfactory openings (olo) and the anterior part of the brain is conjectural. They may have passed through the short canals (sc) across $M_{2/3L}$ and R shown in Pl. 6, fig. 7, but, being very thin structures, they would not normally be traceable. The olfactory system of *M. i. miloni*, in any case, compares closely with that of Heterostraci except that the brain and olfactory sense organs were widely separated.

It is almost certain that the viscera, and very likely the gill slits, would need to be innervated from the brain in *M. i. miloni*. By comparison with vertebrates in general the corresponding nerves would be respectively the paired intestinal branches of the vagus, and the branchial branches of the facial, glossopharyngeal and vagus nerves, all of which, of course, arise from the medulla. With one likely exception there is no direct evidence of these nerves in *M. i. miloni*, but they could well have existed without touching the skeleton. The exception corresponds to the paired nerves n_0 to the ventral skeleton, which, by comparison with *Petromyzon* (Johnston 1905, pl. 5) may possibly represent the non-lateralis component of the hyomandi-

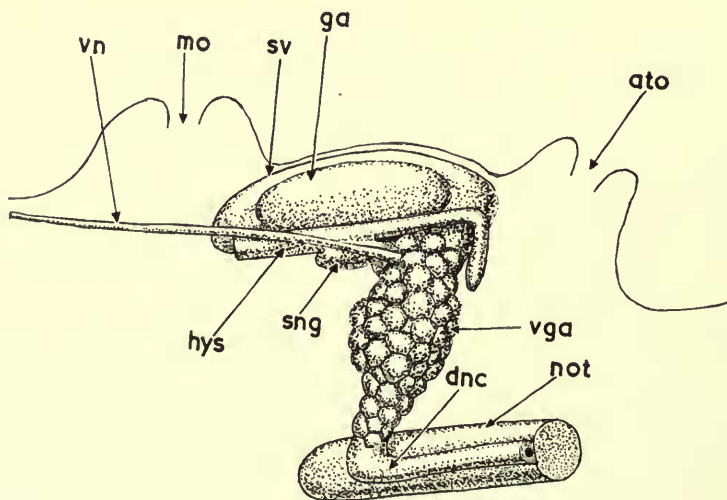


FIG. 22. Brain and associated structures of the tadpole larva of the tunicate *Amaroucium constellatum* (Verrill) (redrawn after Grave, 1921, fig. C). ato = atrial opening ; dnc = dorsal nerve cord ; ga = definitive ganglion ; hys = hypophysis ; mo = mouth ; not = notochord ; sng = subneural gland ; sv = sensory vesicle ; vga = visceral ganglion ; vn = visceral nerve.

bular branches of the facial. It is possible that the nerves n_0 also represent the median-line nerves of cornutes.

The hypophysis of *M. i. miloni* must, as already mentioned, have underlain the lower medial part of the brain (Imp) and have been connected to the buccal cavity by a duct, as it is in tunicates. In echinoderm terms it corresponds in position to the axial sinus plus the water vascular system, i.e. organs arising from the left axo-hydrocoel. The opening into the buccal cavity would correspond to the hydropore. The possibility of this homology was implied by Goodrich (1917).

It is interesting to compare the brain of *M. i. miloni* with that of a tunicate tadpole such as *Amaroucium constellatum* as described by Grave (1921) (cf. Fig. 22). This has a visceral ganglion posteriorly, which joins the dorsal nerve cord. Anteriorly are the sensory vesicle to the right, containing the eye and the statocyst, and the definitive ganglion to the left, in contact with the hypophyseal duct. A visceral nerve runs from the left, anterior corner of the visceral ganglion to the region in front of the oral siphon.

The visceral ganglion of a tunicate tadpole can be compared with the medulla oblongata of vertebrates and the posterior part of the brain of *M. i. miloni*. The visceral nerve corresponds in general to the nerves arising from the medulla, and therefore to the posterior part nerves. The sensory vesicle corresponds to the optic lobes, the optic part of the diencephalon, the optic nerves and the eyes of a vertebrate, and to the upper medial part of the brain, optic nerves (n_3) and eyes of *M. i. miloni*. The definitive ganglion corresponds to the hypophyseal part of the diencephalon of a vertebrate, and therefore to the lower medial part of the brain of *M. i. miloni*. Perhaps the most important differences in the nervous systems of tunicate larvae on the one hand, and vertebrates and mitrocystitids on the other, are the absence in tunicate tadpoles of telencephalon, olfactory nerves and acustico-lateralis system. These differences could easily be due to very small size. The statocyst is likely to be a specialization peculiar to tunicates, and functionally equivalent to the acustico-lateralis system.

In further connection with the optic system Dilly (1964) showed that the outer segments of the visual cells of tunicate tadpoles have fundamentally the same ultrastructure as those of vertebrates, indicating inheritance from a common ancestor. This was confirmed by Eakin (1965), who made a brief survey of the different types of photoreceptors described in the literature and showed how different from all others the tunicate tadpole or vertebrate type was. It is therefore not surprising that *M. i. miloni*, which must be close to the common ancestor of tunicates and vertebrates, had an optic system comparable both with that of a tunicate tadpole and with that of an agnathan.

In summary, it seems that the brain and cranial nerves of *M. i. miloni* fundamentally resembled those of vertebrates in general, and primitive agnathans in particular, and were also comparable with those of tunicate tadpoles. The trigeminal complex, trigemino-profundus ganglia, optic, lateralis and olfactory systems were already developed and the brain was divided into portions that are also recognizable in both fish and tunicate tadpoles.

POSTURE, FEEDING AND MOVEMENT: It is fairly certain that *M. i. miloni* habitually

lay with the big-plated side upwards. The reasons are: firstly, this side corresponds morphologically to the upper side of cornutes (p. 289); secondly, it corresponds to the dorsal side of fish; thirdly, the probably sensory peripheral canals, and the eyes and peripheral grooves of *M. mitra*, were on this side; fourthly, in this position the more heavily armoured side would be upwards, which seems reasonable. The ventral parts of the theca would certainly be partly buried in the bottom.

The posterior stem, is commonly bent ventrally in the fossils as found and would have served as an anchor.

Feeding must have been microphagous, and the position of the mouth suggests a deposit feeder. Water was probably pumped through the pharynx by muscles internal to the flexible anterior ventral skeleton. This implies the existence of a velar valve across the posterior margin of the buccal cavity. Pumping by the ventral wall of the theca would not much disturb the mud beneath but would merely raise and lower the dorsal surface.

The anterior stem is seldom well-preserved in *M. i. miloni*, but could probably flex both vertically, by analogy with *M. barrandei* (p. 293), and horizontally, by analogy with *Mitrocystites mitra* (p. 322). The roughly symmetrical, tadpole-like shape of *M. i. miloni* suggests that the animal could swim forwards by lateral flexing of the anterior stem. The extensive, soft tissue-filled spaces in the skeleton may have assisted swimming by lightening the skeleton.

M. i. miloni could probably also crawl backwards pulled by the ventral flexing of the stem. A backwards direction of crawling is suggested by the direction of imbrication of anterior ventral plates (Fig. 13b; Pl. 4, fig. 8) and the transverse ridges (tr in Fig. 13b; Pl. 4, fig. 8), steeper anteriorly than posteriorly, which cross the posterior ventral part of the theca. Both these features would resist forward movement. Also the ventral muscles of the posterior stem were probably larger than the dorsal ones, suggesting that they delivered the power stroke.

The transverse ridges would be most useful when the animal, in crawling, pulled the posterior stem from the sea bottom. This would tend to push the theca anteriorly and also exert a turning moment on it, so that the postero-ventral surface, where the ridges are, would be driven hard into the mud. There are no yaw prevention structures (anterior appendages or ventral spikes) on *M. i. miloni*, which fact suggests that, in crawling, vertical flexing of the stem was more important than horizontal flexing.

d. *Mitrocystites mitra* Barrande

SYSTEMATIC POSITION: Family Mitrocystitidae (as *Mitrocystella*). Genus *Mitrocystites* Barrande 1887, species *Mitrocystites mitra* Barrande 1887, the type species. For an account of the systematics see Chauvel (1941).

OCCURRENCE: Šarká Beds (Llanvirn Series) and Dobrotivá Beds (Llandeilo Series) of Bohemia. The most useful material, preserved in nodules, comes mainly from the Šarká Beds of Šarká, near Prague, and Osek, near Rokycany. The associated fauna indicates a shallow-water, marine environment.

MATERIAL: Národní Museum, Prague (about 220 specimens); British Museum (Natural History) (11 specimens, E 7517, E 16057-9, E 16061-3, E 16068-9, E 16089); University of Bonn (1 specimen); Museum of Comparative Zoology, Harvard (14 specimens Nos. 565 to 579); Royal Scottish Museum, Edinburgh (1 specimen) 1933.70.23; Sedgwick Museum, Cambridge (2 specimens) A48.926-7.

GENERAL SHAPE AND PLATE NOMENCLATURE: The general shape of *M. mitra* is very like that of *M. i. miloni* but broader. The sides of the theca are not so steep, but slope smoothly into the posterior ventral skeleton.

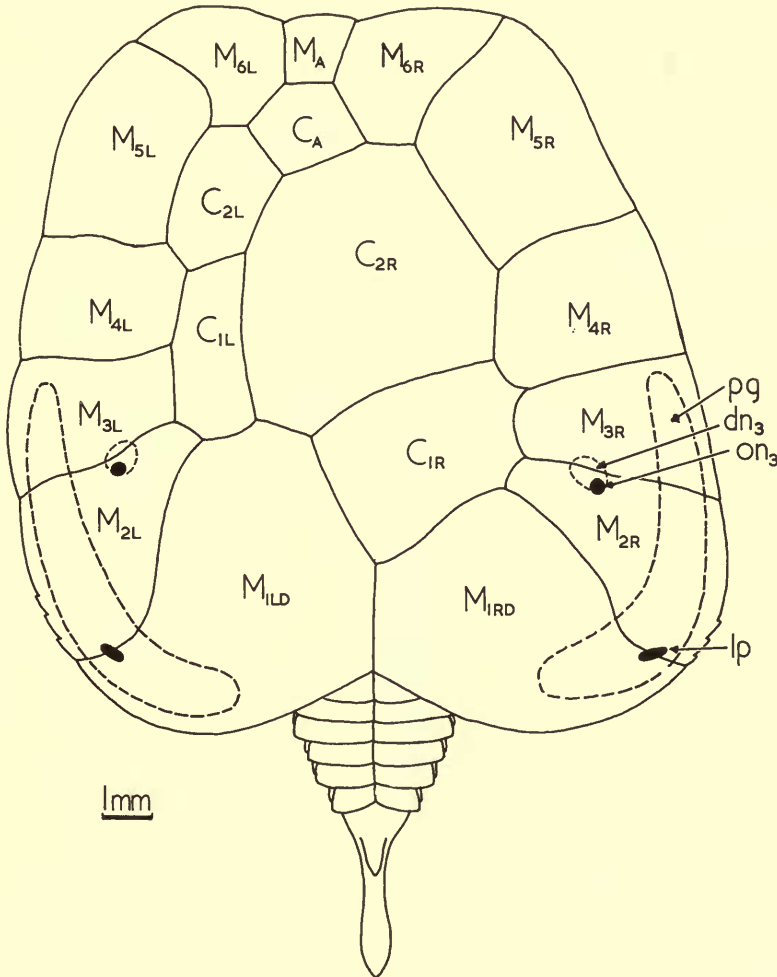


FIG. 23. *Mitrocystites mitra* Barrande. Reconstruction of external features. a. dorsal ; b. ventral ; c. right ; d. anterior ; e. posterior aspects. bo = branchial opening ; dn₃ = depression associated with nerve n₃ (optic depression) ; lp = lateral pore ; mo = mouth ; ng = narrow groove (lateral line) ; on₃ = opening of nerve n₃ (optic nerve) ; or = oral plate ; pg = peripheral groove ; std = styloid ; tr = transverse ridge.

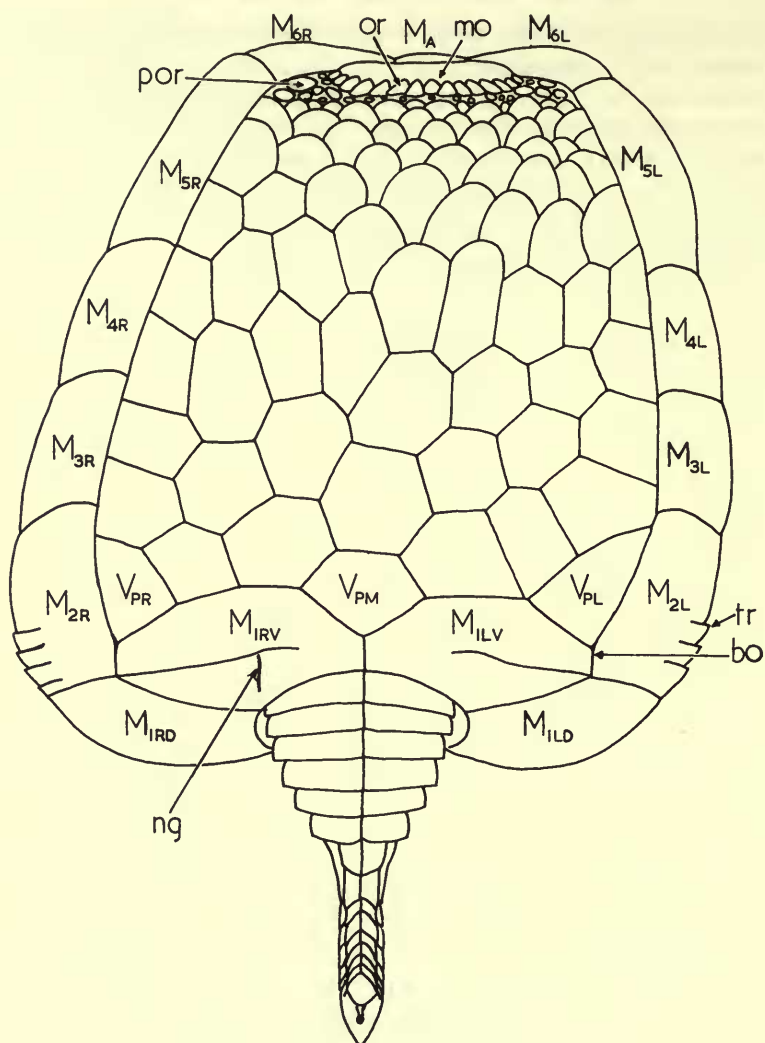


FIG. 23b.

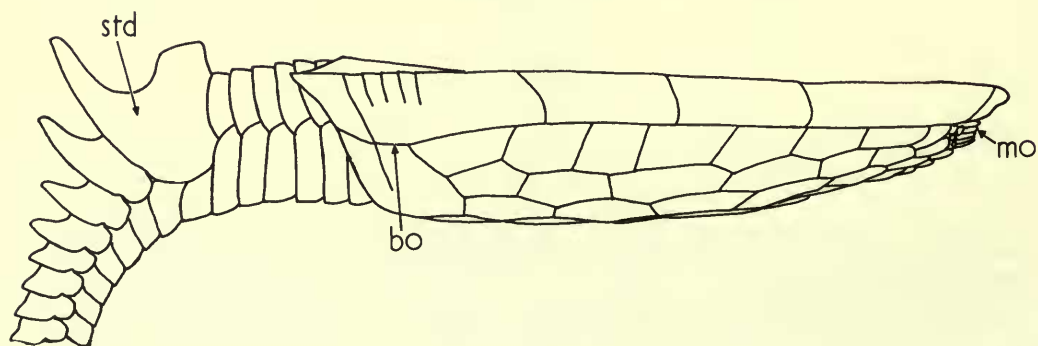


FIG. 23c.

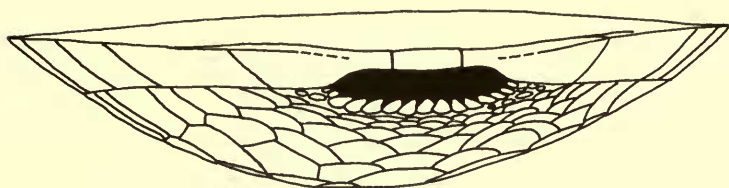


FIG. 23d.

The plates present in the theca are as follows:

Notation	Name	Homologous plate in <i>M. i. miloni</i>
M _{1LV}	Left dorsal 1st marginal	M _{1LD}
M _{1LV}	Left ventral 1st marginal	M _{1LV}
M _{2L}	Left 2nd marginal	M _{2L}
M _{3L}	Left 3rd marginal	? M _{3L}
M _{4L}	Left 4th marginal	? M _{3L}
M _{5L}	Left 5th marginal	M _{4L}
M _{6L}	Left 6th marginal	M _{5L}
M _A	Anterior marginal	M _A
M _{1RD}	Right 1st dorsal marginal	M _{1RD}
M _{1RV}	Right 1st ventral marginal	M _{1RV}
M _{2R}	Right 2nd marginal	M _{2R}
M _{3R}	Right 3rd marginal	M _{3R}
M _{4R}	Right 4th marginal	M _{4R}
M _{5R}	Right 5th marginal	M _{5R}
M _{6R}	Right 6th marginal	M _{6R}
C _{1L}	Left 1st central	—
C _{2L}	Left 2nd central	C _L
C _A	Anterior central	C _A
C _{1R}	Right 1st central	—
C _{2R}	Right 2nd central	C _R
V _{PL}	Left posterior ventral	V _{PL}
V _{PM}	Median posterior ventral	V _{PM}
V _{PR}	Right posterior ventral	V _{PR}
—	ventral plates	ventral plates

THECAL OPENINGS: The mouth is very like that of *M. i. miloni* but the oral plates, which number about fifteen, are shorter. The oral plates carry a hemicylindrical groove on their inner, dorsal faces (hg in Pl. 6, fig. 8) which may have housed a sphincter muscle.

The mouth opens distinctly leftwards in the smallest specimen seen (maximum thecal width 6.4 mm., Pl. 8, fig. 5), and makes an angle of about 12° with a line

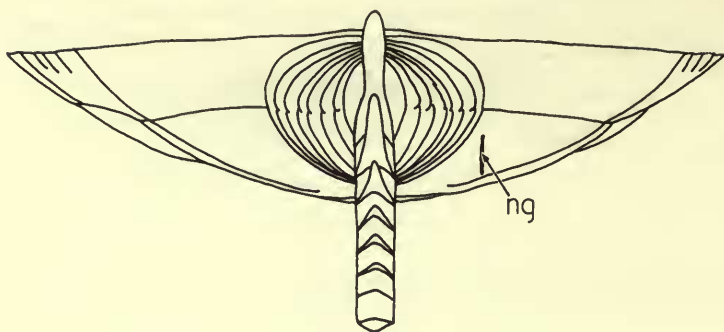


FIG. 23e.

joining the middle of the mouth to the middle of the cerebral depression. This asymmetry is absent from the largest specimens (e.g. Pl. 8, figs. 1, 8) and so, by extrapolation, was presumably even more marked during the earliest phases of life history, before a skeleton was acquired. The mouth also faced leftwards in adult *M. i. miloni* (p. 282, Pl. 5, fig. 2, about 5°) and *Chinianocarpus thoralis* (Ubaghs, 1961a, fig. 1A, B, and personal observation, about 35°) and this is presumably a primitive characteristic of the Mitrocystitidae. It is interesting that the mouth also faces leftwards in larval amphioxus (e.g. Willey 1894 : 143 ff.).

The branchial openings were situated near the posterior right and left corners of the theca (bo in Fig. 23b, c and Pl. 8, figs. 2-4). Pl. 7, figs. 2, 4 show the plates associated with the gill opening on the left side of a single specimen. The break in slope (bsl) in these figures is not explicable if the plates M_{1LV} , M_{1LD} and M_{2L} were merely sutured together, and indicates that the apposed faces of M_{1LV} and M_{1LD} , posterior to the break in slope, were specialised to form articulation facets (af) dorsal and ventral to an articulation. Movement about this articulation would cause a gap to open between the left edge of M_{1LV} , anterior to the break in slope, and M_{2L} , above the gap. As in *M. i. miloni*, there was a median soft layer in the ventral skeleton, continuations of which entered the dorsal skeleton posteriorly and touched the inner faces of the dorsal skeleton laterally. The corresponding parts of the inner faces are excavated to receive the soft layer (sl in Pl. 7, fig. 4). It is apparent that the branchial openings would have been flanked by soft tissue which, as in *M. i. miloni* and *Cothurnocystis curvata*, would have acted as a seal when the opening closed.

The lateral line (ng in Fig. 23b, e, Pl. 8, fig. 3) is situated, as in *M. i. miloni*, on M_{1RV} .

On the dorsal surface are two pairs of openings not present in *M. i. miloni*. The more anterior of these (on_3 in Fig. 23a; Pl. 8, fig. 1; Pl. 10, figs. 5, 7, "paarige Gruben" of Jaekel 1918 : 121) are the openings of the optic nerves (n_3) on to the surface (n_3 are shown in Pl. 7, fig. 4; Pl. 8, fig. 10; Pl. 10, fig. 6). Each opening is often preceded by a small, paired depression across the suture $M_{2/3L}$ and R (dn_3 in Pl. 8, fig. 1) which presumably carried a vesicle on the end of n_3 , i.e. an eye.

The more posterior pair of openings are termed lateral pores (lp in Fig. 23a, Pl. 8, fig. 1; Pl. 10 figs. 4, 5, "Seitenporen" of Jaekel 1918 : 121). They straddle

the sutures M_{1LD}/M_{2L} and M_{1RD}/M_{2R} , and represent the openings on to the surface of nerves n_4 and n_5 (Fig. 27a, b, see also Pl. 6, fig. 6; Pl. 7, fig. 4; Pl. 8, fig. 4 and Pl. 10, fig. 6). The lateral pores are located at the deepest points of paired peripheral grooves (pg) which, though not sharply delimited, are situated near the

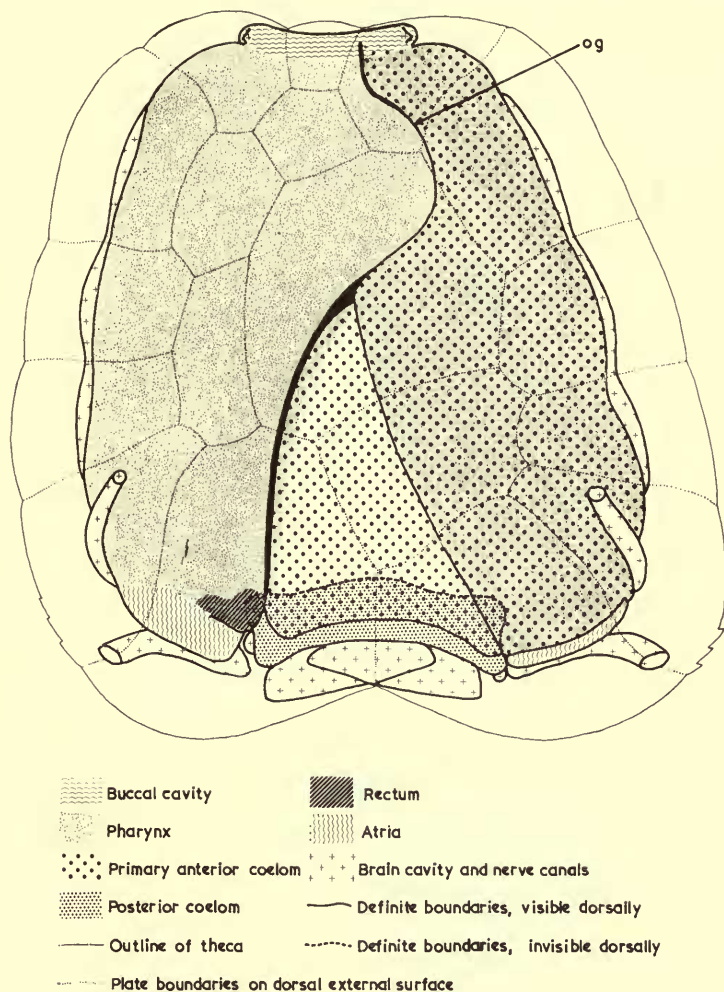


FIG. 24. *Mitrocystites mitra* Barrande. Chambers of the theca, dorsal aspect.
og = oblique groove.

posterior, dorsal edges of the theca. The peripheral grooves are evidently homologous with the peripheral canals of *M. i. miloni* which have the same position and innervation. The surface ornament of the plates is finer under the peripheral grooves than elsewhere (Pl. 10, fig. 5), indicating that in life the grooves probably contained soft tissue.

THE CHAMBERS OF THE THECA: The chambers of the theca differed very little

from those of *M. i. miloni* but the intercameral ridges were less extensively calcified, so that relationships are generally not so well shown.

The oblique groove is basically similar to that of *M. i. miloni* but its anterior end is shallower (cf. Pl. 8, figs. 5, 10 with *M. i. miloni* in Pl. 5, figs. 7, 9). The median branch is well developed (mb in Pl. 8, fig. 10; Pl. 10, fig. 6). The oblique groove just posterior to it is not rounded in the way which, in *M. i. miloni*, suggests contact with the oesophagus (p. 285), but this need indicate only a very small difference in the position of the oesophagus. The separation (grp) between right pharyngeal chamber and residual anterior coelom shows clearly in Pl. 10, fig. 6. The part of the internal mould corresponding to the right pharyngeal chamber

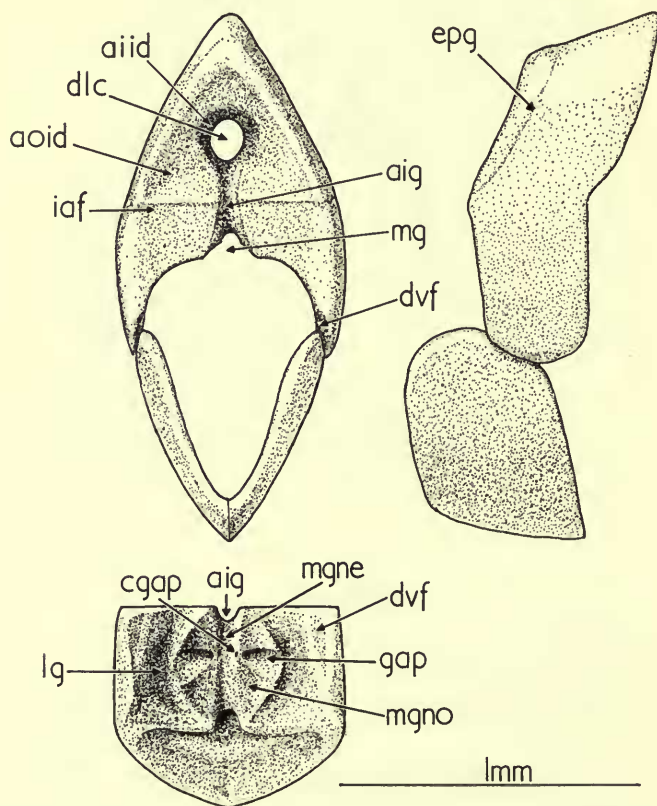


FIG. 25. *M. mitra*. Reconstruction of the skeleton of a segment of the posterior stem. a. anterior aspect ; b. left aspect ; c. ventral aspect of dorsal ossicle ; d. anterior aspect. aig = anterior interossicular groove ; aiid = anterior, inner interossicular depression ; aoid = anterior, outer interossicular depression ; cgap = canal leading to ganglionic pit ; dlc = dorsal longitudinal canal ; epq = epidermal groove ; dvf = dorsoventral facet ; gap = ganglionic pit ; iaf = interossicular articular facet ; lg = lateral groove ; mg = median groove ; mgne = neural part of median groove ; mgno = notochordal part of median groove ; pig = posterior interossicular groove ; piid = posterior, outer, interossicular depression ; poid = posterior, outer, interossicular depression.

carries a series of weak corrugations (sp in Pl. 10, fig. 6) which are absent from the region corresponding to the anterior coelom. These corrugations are sometimes seen in the pharyngeal regions of the internal mould of *M. i. miloni* in large specimens (sp in Pl. 10, fig. 1), and can be compared with the striations on the walls of the pharynx in *Cothurnocystis elizae* (p. 257, sp in Fig. 3B, E; Pl. 2, figs. 2, 5). They may indicate folds in the wall of the pharynx, which would be appropriate for a respiratory and food-collecting organ.

The posterior coelom is very much as in *M. i. miloni*. The rectum, however, left it more anteriorly so that there is no rectal bridge. The rectal ridge is clearly visible (rr in Pl. 10, fig. 6). As in *M. i. miloni* the membrane limiting the posterior coelom seems to have been continuous with that limiting the left pharyngeal

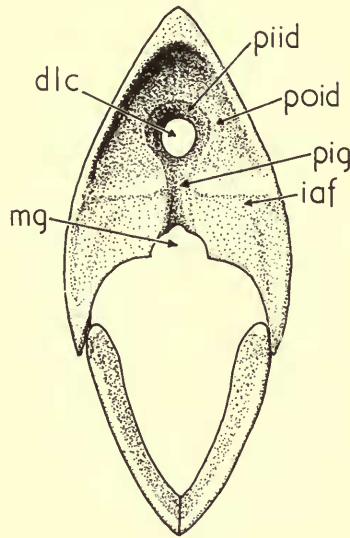


FIG. 25d.

chamber. The two chambers were separated only by a fold in this membrane on the left side of the posterior coelom and this fold became less sharp anteriorly (Pl. 6, fig. 6; Pl. 8, fig. 10).

The left atrium, perhaps because of the more anterior position of the rectum, shows more clearly than in *M. i. miloni* (la in Pl. 6, fig. 6; Pl. 8, fig. 10; Pl. 10, fig. 5). The right atrium is very like that of *M. i. miloni* (ra in Pl. 6, fig. 6).

The buccal cavity (bc in Pl. 8, fig. 10) was much as in *M. i. miloni*, but its wall was less extensively calcified, so that it cannot be dissected out of the internal cast. The olfactory openings (olo in Pl. 8, figs. 5, 10; Pl. 10, fig. 6) occupy exactly comparable positions.

THE STEM: This, again, much resembles that of *M. i. miloni*.

The posterior stem differs externally by having the dorsal ends of the ventral plates everywhere internal to the dorsal ossicles. Paired dorso-ventral facets on

the internal face of the dorsal ossicles (dov in Fig. 25a, c; Pl. 9, fig. 5) are found near the anterior, ventral corners of the ventral plates.

The soft parts are again reflected by the internal sculpture of the dorsal ossicles. The ventral surface of any one of these is traversed by a median groove (Fig. 25a, c) which is divided into an external, notochordal part (mgno) and a more median neural part (mgne). From the neural part a pair of canals goes off in each segment to ganglionic pits (gp). Anterior and posterior interossicular grooves are present in the median plane (aig in Pl. 8, fig. 4). The dorsal longitudinal canal is stouter

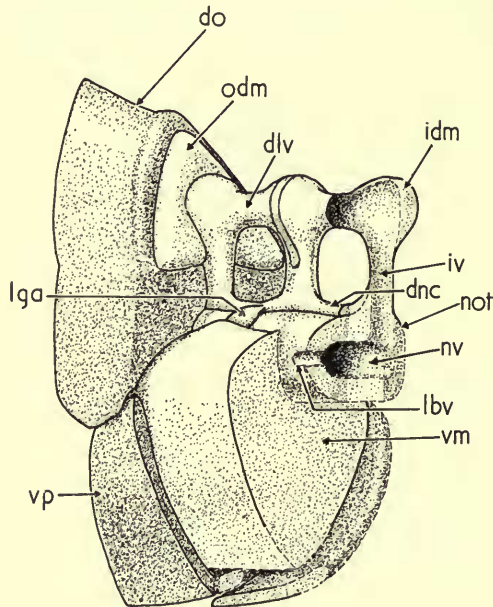


FIG. 26. *M. mitra*. Block diagram of posterior stem. dlv = dorsal longitudinal vessel; dnc = dorsal nerve cord; do = dorsal ossicle; idm = inner dorsal muscle; iv = interossicular vessel; lbv = lateral blood vessel; lga = lateral ganglion; not = notochord; nv = notochordal vessel; odm = outer dorsal muscle; vm = ventral muscle; vp = ventral plate.

than in *M. i. miloni*. The interossicular articulations are situated as in *M. i. miloni*. Anterior and posterior, inner and outer, interossicular depressions exist (aiid, aoid in Pl. 6, fig. 9; aiid, aoid, piid, poid in Fig. 23a, c, d). The outer depressions are shallower and wider than in *M. i. miloni* and the inner depressions relatively much smaller.

A natural mould of the ventral surface of the dorsal ossicles (Pl. 9, fig. 5) gives a representation of the soft parts. Here again a dorsal nerve cord (dnc) overlies a notochord (not) and gives rise to paired, pear-shaped ganglia (ga). In some parts of the specimen it can be seen that the ganglia were connected proximally to the dorsal nerve cord and not to the notochord.

The notochord was laterally compressed, where the apposed interossicular grooves came off but widened beneath the ganglia. Apposed interossicular grooves presumably carried an interossicular vessel going up through the dorsal nerve cord to a vessel in the dorsal longitudinal canal. The lateral widenings of the notochord may indicate lateral vessels coming off the notochord ventral to the skeleton. A reconstruction of the soft parts of the posterior stem is shown in Fig. 26.

Medial and anterior stems differ little from those of *M. i. miloni*, but the anterior stem had only six segments. On some specimens (Pl. 8, fig. 1; Pl. 10, fig. 7) the position of burial suggests that the anterior stem could flex from side to side.

THE BRAIN AND CRANIAL NERVES: The skeletal histology of *M. mitra*, which affects the reconstruction of the cranial nerves, differs in some respects from that of *M. i. miloni*. Thus: 1. The median soft layer of the ventral skeleton (sl in Pl. 10, fig. 8) was not dilated where nerves passed through it. 2. All plates of the ventral skeleton, not only the more posterior ones, have an inner layer of calcite (il in Pl. 10, fig. 4). It can therefore be shown that there was no soft layer of connective tissue just within the outer calcite layer in the anterior ventral region. There is no evidence concerning this point in *M. i. miloni*. 3. There were no irregular, soft-tissue filled spaces in the dorsal skeleton. 4. As already mentioned (p. 315), the intercameral ridges were less extensively calcified than in *M. i. miloni*. 5. The outer surfaces of the central dorsal plates sometimes show near their centres (Pl. 8, fig. 1, fp.) a patch preserving the coarse fenestration of the juvenile skeleton (cf. Pl. 8, fig. 5 and the developing calcite plates of crinoids shown by Seeliger 1892).

Three of these features make the reconstruction of the cranial nerves more difficult than in *M. i. miloni*, namely the absence of dilatations in the ventral soft layer and of spaces in the dorsal skeleton, and the less extensive calcification of the intercameral ridges. Nonetheless, the two nervous systems were clearly very similar and the detailed differences are of much interest.

The anterior part of the encephalic cast is much smaller than in *M. i. miloni* (ap in Fig. 27a-c; Pl. 8, fig. 9), and takes the form of a crinkling of the median posterior dorsal suture (M_{1L}/RD). This crinkling is absent from all other sutures and is therefore unlikely to represent a mere strengthening device.

The medial part of the encephalic cast is more clearly demarcated in dorsal aspect from the posterior part of the cast than in *M. i. miloni* (Fig. 27a; Pl. 6, fig. 6; Pl. 8, fig. 10; Pl. 10, fig. 6; cf. Pl. 6, fig. 1; Pl. 10, fig. 3 for *M. i. miloni*). Its foramen (mpf in Fig. 27b, Pl. 9, fig. 6) is much wider than in *M. i. miloni* (Fig. 19b; Pl. 6, fig. 4) and grooves on the front of the hypocerebral processes (gmpn in Pl. 8, fig. 6) indicate the proximal courses of the medial part (optic) nerves. It therefore follows that the optic part of the brain and the bases of the optic nerves were relatively bigger in *M. mitra* than in *M. i. miloni*. This recalls that, more peripherally, the optic nerves (n₃) were much bigger in *M. mitra* and continued on to the dorsal surface of the theca, where each one ended in a vesicle or eye. In *M. i. miloni*, on the other hand, the eyes, if they existed at all, were only vestigial and the optic nerves, at least in the adult, did not connect with them. All parts ascribed to the optic system were therefore better developed in *M. mitra* than in *M. i. miloni*, which confirms that they had a common function.

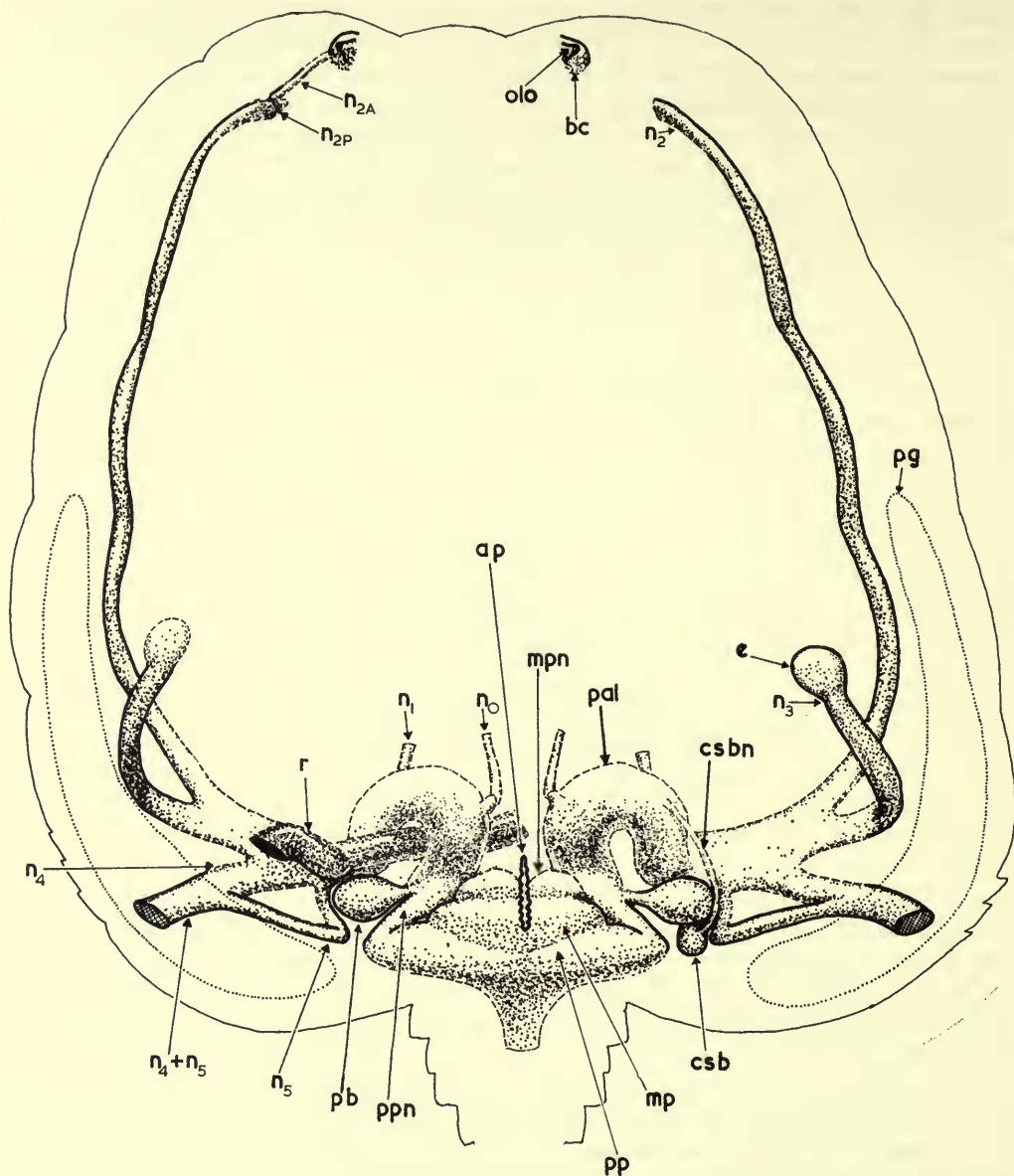


FIG. 27. *M. mitra*. Reconstruction of brain and cranial nerves. a. dorsal aspect; b. anterior aspect of posterior part; c. left aspect for right part; ap = anterior part of brain; bc = buccal cavity; csb = carrot-shaped body (lateral line ganglion); csbn = nerve to carrot-shaped body (nerve to lateral line ganglion); e = eye; lmp = lower medial part of brain; mp = medial part of brain; mpf = medial part foramen; mpn = median part nerves; n_0 = nerve leaving posterior coelom, near mid line; n_1 , 2A, 2P, 3, 4, 5 = nerves of palmate complex; olo = olfactory opening; pal = palmar nerve; pb = pyriform body; pg = peripheral groove; pp = posterior part of brain; ppn = posterior part nerve; r = rectum; ump = upper medial part of brain.

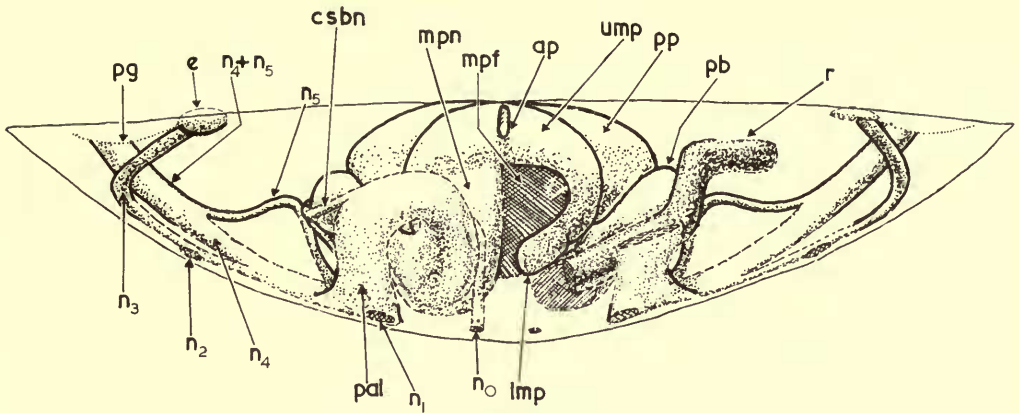


FIG. 27b.

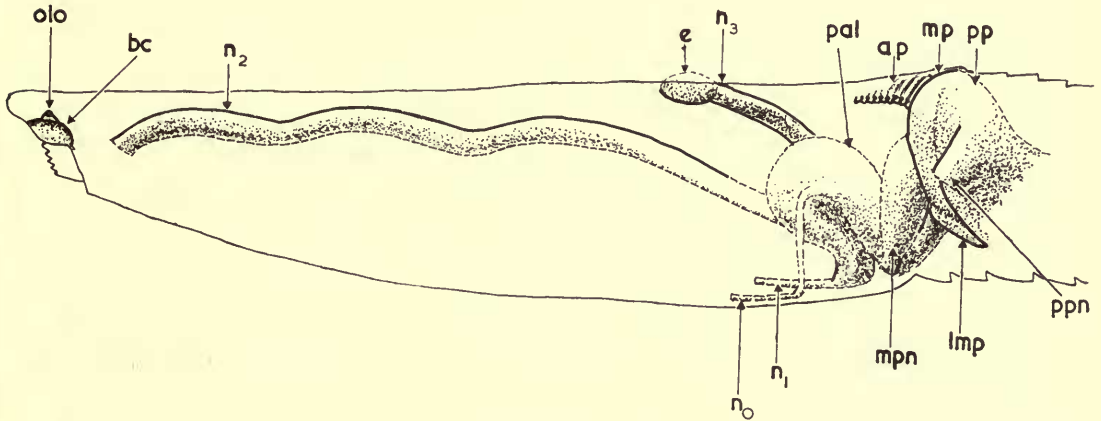


FIG. 27c.

The lower medial, or hypophyseal, part of the encephalic cast, as already mentioned, is slightly swollen in *M. mitra* (Pl. 9, fig. 6) differentiating it from the optic part of the encephalic cast.

The posterior part of the encephalic cast scarcely differs from that of *M. i. miloni*.

Turning to the palmate complexes, the palmar nerves (pal in Fig. 27a-c) did not cause the front wall of the posterior coelom to calcify so extensively as in *M. i. miloni* and consequently these nerves cannot be traced until they had already begun to enter the ventral skeleton. Their courses at these points were nearly vertical (pal in Pl. 10, fig. 8) as in *M. i. miloni*, and the left one presumably looped over the rectum as in that form.

Of the branches arising from the palmar nerves, left and right n_1 , because of the absence of dilatations in the ventral, soft layer, cannot be demonstrated in *M. mitra*, though they doubtless existed. The nerves n_2 are most proximally indicated in one specimen (Pl. 10, fig. 8) just before the left one left M_{1LV} . They must have

run through V_{PL} and R and left the ventral skeleton with the soft layer. They can be traced again on the inner faces of M_{2L} and R and then followed a course indicated by left and right grooves in the skeleton, much as in *M. i. miloni*. Anteriorly the grooves turn abruptly downwards in the middle of M_{5L} and R , and at these points the nerves must normally have left the dorsal skeleton. In one specimen, however, the left groove bends horizontal again and runs forward as far as the anterior end of M_{5L} (Pl. 8, fig. 10). This suggests that left n_2 divided into two branches (n_{2A} and n_{2P} in Fig. 27a). n_{2P} was thicker and innervated the anterior part of the belly. n_{2A} was thinner and probably innervated the mouth and lower lip. The parts of the ventral skeleton innervated by these two branches can be estimated by comparing Pl. 8, fig. 8 and Pl. 8, fig. 10. There is no evidence as to whether right n_2 had comparable branches at its anterior end.

The nerves n_3 of the palmate complex, or optic nerves, can in one case be traced for a short distance in the ventral skeleton on the left side (Pl. 10, fig. 8). The canal which here carried left n_3 was compressed in section. The nerves n_3 left the ventral skeleton with the soft layer (Pl. 7, fig. 4) anterior to the branchial opening. They then travelled upwards and forwards in paired grooves (Pl. 6, fig. 6; Pl. 7, fig. 4; Pl. 8, fig. 10 and Pl. 10, fig. 6) which gradually deepened, leading finally to short cylindrical canals (Pl. 7, fig. 4) that opened (on_3) on the dorsal surface. The changes in section of the nerves n_3 —compressed in the ventral skeleton, becoming circular peripherally—strongly confirm that the structures were indeed nerves.

The two pairs of nerves n_4 and n_5 must have had courses in the median layer of the ventral skeleton very similar to those in *M. i. miloni*, though their exact positions cannot be defined. The nerves entered M_{1L} and RD with the median soft layer, much as in *M. i. miloni*. Immediately afterwards the nerves n_5 swung outwards to join n_4 (Fig. 27a, b; Pl. 8, fig. 10; Pl. 10, fig. 6) and n_4 and n_5 then on both sides ran upwards together, into the lateral pores, to innervate the peripheral grooves.

The pyriform bodies and lateral-line ganglia are much as in *M. i. miloni* except that the pyriform bodies were more symmetrical. The dorsal and ventral cupules enclosing the left pyriform body show in Pl. 8, figs. 2, 4. The lateral-line ganglion (csb) is shown in Pl. 10, fig. 8.

The olfactory nerves must have consisted, as in *M. i. miloni*, of isolated fibres in the dorsal skeleton connecting the olfactory openings (olo) in the buccal cavity with the telencephalon (ap).

The nerves n_0 , in the absence of dilatations of the ventral soft layer, cannot be demonstrated in *M. mitra* but no doubt existed.

In summary, therefore, some features of the cranial nerves show more clearly in *Mitrocystites mitra* than in *M. i. miloni*. These features relate mainly to the optic system, the anterior end of the left maxillary trigeminal (n_3) and the hypophyseal part of the brain (lmp). Some details of the dorsal sensory complex (i.e. peripheral grooves and n_4 and n_5) also differ.

POSTURE, FEEDING AND MOVEMENT: *M. mitra* must have resembled *M. i. miloni* in posture, feeding and movement. Some specimens (Pl. 8, fig. 1; Pl. 10, fig. 7) show more clearly than in *M. i. miloni* that the proximal stem could bend from side

to side. The theca probably lay more deeply buried in the mud than that of *M. i. miloni* since there is no sharp "change in slope" between marginal plates and posterior ventral skeleton, and the transverse ridges are restricted to the higher parts of the theca. The theca of *M. mitra* can be compared with the shell of the Recent bivalve *Pecten maximus*, which habitually lies with the convex valve downwards, and with the flat valve about level with the sea-floor.

IV. DISCUSSION

a. *Cornutes and Mitrates*

The imperfection of the fossil record makes it impossible to reconstruct the phylogeny of cornutes and mitrates in detail. Only one species of cornutes is known from the Middle Cambrian, whilst none is known from the Upper Cambrian. Five specimens (placed in two species and genera) are known from the Lower Tremadoc Series (Ubaghs 1963). In the Upper Tremadoc the cornute record is better but incomplete, since only one specimen is known from outside Europe (Gigout 1954). The only later cornutes described in the literature are those from the Ashgill Series of Scotland.

The record of the earliest mitrates is little better. The two earliest families, the Lagynocystidae and Mitrocystitidae, are both first known from the Upper Tremadoc or Lower Arenig Series. The species which represent those families at this horizon (*Peltocystis cornuta* Thoral and *Chinianocarpos thorali* Ubaghs) resemble each other enough to suggest a common origin from the cornutes. They also differ enough to indicate a long, unrecorded period of divergence. In later rocks the mitrates are fairly common, though they have not received much attention.

Nonetheless certain deductions concerning the phylogeny of cornutes and early mitrates are possible, despite this lack of fossils. Firstly, the cornutes and mitrates are certainly closely related to each other, and the establishment of a group to contain both (Class Stylophora, Subphylum Calcichordata) is justified. Secondly, the mitrates certainly arose from the cornutes, rather than the converse. Thirdly, the line of descent from the earliest known cornute (*Ceratocystis*) to *Mitrocystites* and *Mitrocystella* can be postulated from known forms. This reconstructed line of descent is essentially a working hypothesis, and although not entirely consistent with the stratigraphical order of first known occurrences, one must keep in mind the patchy fossil record. The Lagynocystidae are not further considered here, and until they have been studied in detail it is pointless to fit them into a general scheme.

The close relationship of cornutes and mitrates is indicated by a number of features in common: 1. Both groups had a mouth near the front end of the theca. 2. In both groups the skeleton was made of plates, each a single calcite crystal. 3. Both groups had a flattened theca, adapted for lying on the sea-floor, with dorsal and ventral surfaces. 4. Both groups had marginal plates, usually numbering twelve to fifteen, round the theca. Thus, counting dorsal and ventral first marginals, but excluding appendages, *C. elizae* had thirteen marginals, *C. curvata* had twelve, *Chinianocarpos thorali* had twelve, *M. i. miloni* had fourteen and *M. mitra* fifteen.

5. Both groups had a basically similar arrangement of thecal chambers. 6. Both groups had a brain and paired pyriform bodies at the anterior end of the stem. 7. In both groups the stem ended abruptly. 8. In both groups an anterior, tetraserial part of the stem was adapted for flexing sideways and a posterior part for flexing vertically. 9. Within the stem, both groups certainly had segmented muscle blocks and a chambered organ or notochord and both almost certainly had a peduncular nerve (dorsal nerve cord). 10. Both groups were pharyngotrematous. Cornutes had external branchial slits; Mitrates had presumed internal branchial slits and branchial openings. 11. Most cornutes had the anus, either internal or external, just left of the stem while mitrates had the anus internal and just left of the stem. Against this, however, the earliest known cornute (*Ceratocystis perneri*) had the anus right of the stem (personal observation).

That mitrates were descended from cornutes, rather than the converse, is indicated by the fact that: 1. The earliest known cornute is Middle Cambrian in age, while the earliest known mitrates are Upper Tremadoc or Lower Arenig Series. 2. The mitrates give the impression of imperfect bilateral symmetry, imposed on a basic, cornute-like asymmetry. 3. One of the earliest known mitrates (*Chinianocarpus thorali*) has many cornute-like features, i.e. big plates just ventral to the mouth, a partly flexible thecal roof, an oblique groove borne entirely on marginal plates, not very massive dorsal stem ossicles, the ability to flex the posterior stem upwards, and a very short lateral line. The mitrates probably arose from the cornutes during the Upper Cambrian.

The line of descent from *Ceratocystis* to *Mitrocystites* and *Mitrocystella* can be reconstructed as follows:

1. *Ceratocystis*. Theca boot-shaped, rigid. Anterior appendages present. Anus external, right of the stem. Gill slits external, left of the stem. No lateral line. Only known occurrence, Middle Cambrian (*Ceratocystis perneri* Jaekel).

2. *Cothurnocystis (americana)* type). Theca boot-shaped. Floor of theca rigid. Roof of theca a flexible integument. Anterior appendages not known. Anus not known. Gill slits external, left of stem. No lateral line. Only-known occurrence, Lower Tremadoc Series.

3. *Cothurnocystis (elizae)* type). Theca boot-shaped. Floor of theca an integument crossed by a strut. Roof of theca a flexible integument. Anterior appendages present. Anus external, left of the stem. Gill slits external, left of stem. No lateral line. First known occurrence, Upper Tremadoc or Lower Arenig Series (*C. primaeva* Thorall).

4. *Phyllocystis*. Theca leaf-shaped. Floor of theca an integument crossed by a thin, curved and probably functionless strut. Roof of theca a flexible integument. Anterior appendages absent. Anus external, left of the stem. Gill slits external, left of the stem. No lateral line. First known occurrence Lower Tremadoc Series (*Phyllocystis* sp., Ubahgs 1963).

5. *Chinianocarpus*. Theca leaf-shaped. Floor of theca an integument with no strut. Roof of theca mainly rigid, with a small area of integument. Anterior appendages absent. Anus internal, left of stem. Gill slits internal, paired. Lateral line a small pit. Only known occurrence Upper Tremadoc or Lower Arenig Series (*C. thorali* Ubahgs 1961a).

6. *Mitrocystites* & *Mitrocystella*. Theca leaf-shaped. Floor of the theca an integument with no strut. Roof of theca entirely rigid. Anterior appendages absent. Anus internal, left of stem. Gill slits internal, paired. Lateral line a groove. First known occurrence Llanvirn Series (*Mitrocystites mitra* Barrande and *Mitrocystella barrandei* Jaekel).

The line of descent represented by *Cothurnocystis curvata* probably arose from a *C. elizae*-like ancestor. In most respects *C. curvata* differs more from *Ceratocystis perneri* than does *C. elizae*. Thus, unlike both *C. perneri* and *C. elizae*, *C. curvata*: 1. Has no right oral appendage. 2. The anus is internal. 3. The mouth is dorsal, instead of anterior. 4. The anterior margin is strongly convex upwards. 5. The stylocone tapers very abruptly. In addition, the branchial skeleton of *Ceratocystis perneri* needs little modification to produce that of *C. elizae*. It needs much modification, on the other hand, to produce that of *C. curvata*. The earliest-known representative of the *C. curvata* group, like that of the *C. elizae* group, is Upper Tremadoc or Lower Arenig in age (Ubaghs, personal communication). The internal anus may be a genuine point of comparison with mitrates, or may have been acquired independently.

The changes involved in going from *Cothurnocystis* of *elizae* type, through *Phyllocystis* and *Chinianocarpus* to *Mitrocystites* or *Mitrocystella* are worth stating in detail, since this course of evolution includes the origin of mitrates from cornutes.

1. Mouth

- i. A big plate (M_A) developed dorsal to the mouth, as in *C. thorali*.
- ii. Subsequently the big plates forming the ventral mouth frame (M_{5R} , M_{6L} of *C. elizae*, M_{5R} , M_{4L} of *C. thorali*) became reduced, so that they no longer met at the mid-ventral line. At about the same time M_A fused to these same plates.
- iii. Presumably later than (i), the oral plates of the upper lip were lost.

2. Thecal shape and skeleton of theca

- iv. Appendages and anterior ventral spikes were lost, as in *Phyllocystis*.
- v. At about the same time the theca became more symmetrical, as in *Phyllocystis*.
- vi. Somewhat later than (iv) and (v) the posterior, ventral spikes were lost. They are present but weak in *Phyllocystis*.
- vii. The strut, which had functioned to prevent collapse of a concave anterior margin when the muscles of the integuments contracted, was lost. When this margin became convex, the strut lost its function. In *Phyllocystis* it is, accordingly, very slender and curved. It is absent in *Chinianocarpus thorali* where, as compared with *Phyllocystis*, the roof of the theca is more rigid and the floor is not in one plane.
- viii. The marginal plates grew forward from the posterior, right-hand part of the theca, carrying the oblique groove with them, as in *C. thorali*.

3. Thecal chambers and gill slits

- ix. The right pharyngeal chamber pouched out from the left one, and right gill slits appeared. In addition the right atrium and gill opening appeared, if the gill slits were already internal.

x. The pharyngo-visceral line (oblique groove) and anterior coelom came to be fixed to the ceiling of the theca. This could have been either the precondition for, or the result of, the appearance of the right pharyngeal chamber (ix). It was connected with the expansion of the right, posterior, marginal plates (viii).

xi. The atria appeared. Right and left atria probably arose simultaneously if the right gill slits had appeared already (ix). Otherwise the left atrium preceded the right one.

4. *Stem*

xii. The posterior stem developed the ability to flex downward as well as upward.

xiii. In connection with this, the ventral posterior stem ossicles became less massive and were finally reduced to paired ventral plates, and the stylocone disappeared. Conversely, paired dorsal plates fused, giving rise to massive ossicles. Interossicular articulations appeared, and then, later, the styloid arose by fusion of the two most anterior of these ossicles.

xiv. Subsequently the posterior stem lost the ability to flex upwards.

5. *The brain and cranial nerves*

xv. The first dorsal marginals enlarged and grew backwards, so enveloping the front of the brain and the dorsal sides of the pyriform bodies.

xvi. At about the same time the first ventral marginals became separated from the brain, though they retained contact with the pyriform bodies.

xvii. The optic nerves pushed upward and opened on to the dorsal surface.

xviii. The lateral line and its nerve supply appeared.

xix. The palmate complexes either arose or, as seems more likely, became enclosed in skeleton.

xx. The olfactory system either arose or became enclosed in skeleton.

Changes in the stem and theca can be explained by changes in the manner of movement. When an animal like *C. elizae* crawled backwards by sideways flexing of the anterior stem, the anterior rigid appendages and the ventral spikes prevented yaw and resisted forward slipping (p. 265). Such a form as *Phyllocystis*, with weak, posterior ventral spikes, a symmetrical theca and no anterior appendages or anterior ventral spikes, probably crawled backwards by flexing the anterior stem downwards, so pushing the rather stiff posterior stem anteriorly and ventrally into the mud. Yaw prevention devices would not be needed and were lacking. The weak posterior ventral spikes would function during the return stroke of the stem, which would exert a turning moment on the theca. This moment would push the posterior theca, where the spikes were, into the mud and prevent the theca from slipping forwards.

The mitrate ability to flex the posterior stem ventrally, with all its related changes, developed because this helped the anterior stem in the work of pulling the theca backwards. The transverse ridges on the postero-ventral surface of the theca of mitrates served the same function as the posterior ventral spikes of *Phyllocystis*.

In conclusion, the broad way in which cornutes and mitrates are related is fairly clear. Large morphological gaps remain to be filled, however, partly by new collecting, and partly by re-examining old material.

b. *Stylophora*, *echinoderms*, *hemichordates* and *chordates*

The relations of *Stylophora* with other groups, and the proposal to transfer them from the Echinodermata to the Chordata as Subphylum Calcichordata, will now be discussed. This reallocation is less radical than at first appears, since zoologists agree that echinoderms and chordates are related. The Hemichordata are here regarded as a phylum separate from, though related to, the Chordata, following Barrington (1965) and Hyman (1959).

The zoological argument relating echinoderms and chordates has three aspects. The first links echinoderms and hemichordates, the second links hemichordates and chordates, and the third links echinoderms and chordates directly.

The aspect of the argument linking echinoderms and hemichordates can be stated as follows:

1. Both groups have radial cleavage. 2. Both sometimes have similar larvae. 3. In both, the blastopore becomes the larval anus. 4. Both are tricoelomatous. 5. In both, the protocoele develops an opening to the exterior on the left side of the larva. 6. In both, a pulsatile vesicle (heart of hemichordates, madreporic vesicle of echinoderms) arises in close association with the protocoele (Narasimhamurti 1931 : 484, and earlier authors). The argument relating hemichordates and echinoderms is well summarised by Hyman (1959 : 197). A most elaborate series of echinoderm, hemichordate homologies was proposed by Gemmill (1914 : 277).

The aspect of the argument linking hemichordates and chordates depends mainly on the presence of gill slits in both groups (Hyman 1959 : 201). In addition, both can have a collagen-rich mesodermal skeleton, are deuterostomatous and have radial cleavage.

The third aspect of the argument, which links echinoderms and chordates directly, depends on the presence in both groups of radial cleavage, a mesodermal skeleton and deuterostomy, and the possible broad homology of water vascular and hypophyseal systems (Goodrich 1917).

The relationship between *Stylophora* and echinoderms, though less close than that with the chordates, is not in doubt. *Stylophora*, like all echinoderms, have a skeleton in which each plate is a single crystal of calcite. In addition, anterior and posterior coeloms of *Stylophora* may correspond to left and right somatocoels in echinoderms. Further, the *Stylophora* have a particular relationship with stalked echinoderms (Crinozoa, Matsumoto 1929) since: 1. In both groups there is a stem. 2. Both groups have a chambered organ and peduncular nerve in the stem, an aboral nerve centre oral (anterior) to it and nerves radiating from the aboral nerve centre to the theca. 3. Both groups have the mouth at the end of the theca farthest from the stem. 4. Among Crinozoa, crinoids at least are typically attached by the distal end of the stem. The abrupt end of the stem of *Stylophora*

strongly suggests fracture and may indicate that a larval stylophoran attached by a hold-fast at the end of the stem, from which it subsequently broke away. 5. The vestibule of crinoids may correspond to the buccal cavity of Stylophora. 6. The broad lumen of the anterior stem of Stylophora compares with a similar broad proximal lumen in solute "carpoids", many primitive crinoids, and many eocrinoids and rhombiferan cystoids. The Stylophora differed from echinoderms most importantly by having branchial slits and no obvious water vascular system.

Crinozoa may possibly have arisen from Stylophora by the loss of branchial slits, rather than the converse. The same line of speculation suggests that Stylophora may have derived directly from Hemichordata.

Turning now to the chordate affinities of the Stylophora, of the forms here studied the Mitrocystitidae, in particular, in many ways resemble tunicate tadpoles. Thus: 1. Both are clearly divided into a body (theca) and a postanal tail (stem). 2. Both have a dorsal nerve cord resting directly on a notochord, the latter confined to the stem or tail. 3. Mitrocystitidae and appendicularian tadpoles (Martini 1909) have paired segmental ganglia in the stem or tail. 4. The brain of Mitrocystitidae had hypophyseal, optic and medullary parts which can also be recognised in tunicate tadpoles. 5. Both Mitrocystitidae and tunicate tadpoles have paired atria. 6. Both Mitrocystitidae and tunicate tadpoles have the rectum opening into the left atrium.

It should be emphasized that tunicate tadpoles resemble mitrates rather than cornutes in the paired atria and gill slits, the rectum opening into the left atrium and the subdivisions of the brain. A mitrocystitid, in fact, could be briefly described as a giant, calcite-plated tunicate tadpole. Pending further study, it is uncertain how far this description would also apply to a lagynocystid mitrate. If, as argued below, the extant chordate subphyla have risen only once from the Stylophora, then there are arguments which suggest that the Mitrocystitidae rather than Lagynocystidae were their point of origin.

Mitrocystitidae most differed from tunicate tadpoles, apart from size, in the abruptly ending stem with its posterior portion adapted to vertical flexion, the calcite skeleton and the blood system of the stem. Further, larval Mitrocystitidae, like Stylophorans in general, may have been anchored for a time by the posterior end of the stem. Tunicate larvae, on the other hand, attach by adhesive papillae, at the anterior end of the body, which may possibly be homologous with the cement glands of many fish and amphibians.

Relationship between Cephalochordata and Mitrocystitidae is indicated by the following points: 1. Both groups have a dorsal nerve cord and notochord, and segmentally repeated muscle blocks in a postanal tail. 2. Both groups have internal gill slits, with, probably in both, the left ones appearing before the right ones in ontogeny. 3. The left-facing mouth of larval amphioxus can be compared with that of mitrocystitids. Relationships of cephalochordates with mitrates more than with cornutes is suggested by the paired, internal gill slits, with the left ones appearing first in ontogeny. Relationship with primitive mitrocystitids rather than lagynocystids or advanced mitrocystitids is particularly indicated by the

left-facing mouth, for, of all known Stylophora, *Chinianocarpus thoralis* has the most left-facing mouth, while lagynocystids have the mouth facing right.

Cephalochordates differ most obviously from mitrates in that: 1. They lack a calcite skeleton. 2. The tail is entirely adapted for lateral flexion and does not end abruptly. 3. The longitudinal caudal blood vessels are ventral to the notochord. 4. Myotomes, notochord and dorsal nerve cord extend to the front end of the animal. 5. Segmental (dorsal root) ganglia are lacking and ventral spinal roots exist. 6. There is no brain. 7. The anus, though facing left, is external. 8. Anterior, larval adhesive organs, which were presumably lacking in mitrates if the larvae attached by the stem, have been reported in *Amphioxus* (van Wijhe 1925).

Mitrocystitidae resemble Agnatha in the following ways: 1. In both groups the dorsal nerve cord is dorsal to, and rests on, the notochord and gives rise to paired segmental ganglia (dorsal root ganglia of agnathans). 2. Both groups have segmented muscle blocks in the postanal stem or tail. 3. In both groups the brain lies at the anterior end of the notochord and can be divided into medullary, optic, hypophyseal and olfactory portions. 4. In both groups the cranial nerves include olfactory, lateralis, optic and trigeminal complexes. In both the trigeminal complex has trigemino-profundus ganglia and probably mandibular and maxillary branches. 5. Both groups have paired gill slits.

Paired gill slits and the subdivisions of the brain and the cranial nerves connect the agnathans with the mitrates rather than the cornutes, and the existence of the lateralis complex connects Agnatha with Mitrocystitidae rather than Lagynocystidae.

Among agnathans, the earliest and most primitive Heterostraci (Cyathaspididae) are particularly linked with Mitrocystitidae by having paired gill openings, small eyes, paired olfactory nerves opening into the roof of the buccal cavity, no pineal eye, and primitively marine habitat (Denison 1956, 1964; White 1958).

The most important differences between Mitrata, in particular Mitrocystitidae, and Agnatha are: 1. Agnathans, like vertebrates and other extant chordates, have a uniform tail, not ending abruptly, with the longitudinal caudal vessels ventral to the notochord. 2. If agnathans have a hard skeleton it is formed mainly of hydroxyapatite, not calcite. This is true of vertebrates in general, whose only purely calcitic parts are the otoconiae of the acustico-lateralis system. 3. The spinal nerves of agnathans have separate dorsal and ventral roots. 4. The anus of agnathans is median and external. 5. The brain of agnathans is longer and extends farther forward. 6. Agnathan eyes are often better developed. 7. The acustico-lateralis system of Agnatha includes ears.

Two features that the earliest agnathans may have lacked, although they occur in most vertebrates, were a closed circulatory system and oculo-motor muscles, for both these features are absent in myxinooids.

As regards larval attachment, recently hatched anuran tadpoles and the young larvae of many archaic living fish such as dipnoans, *Polypterus*, *Amia*, *Lepisosteus* and *Acipenser* attach themselves by cement organs near the anterior end of the body (Kerr 1919, esp. p. 178 ff.). These organs are likely to be homologous in all

the cases cited and, as already mentioned, they may possibly be homologous with the adhesive papillae of tunicate tadpoles. They may also be homologous with the adhesive papillae reported in amphioxus.

The evidence for a relationship between Stylophora and the extant chordate subphyla can therefore be summarised by saying that all Stylophora had branchial slits, a stem (or tail) which is post-anal and contains segmental muscle blocks, a notochord with a brain at the front of it, and a mouth at the front end of the body. Furthermore the Mitrocystitidae, at least, resembled extant chordates in having paired branchial slits, dorsal nerve cord and segmental ganglia. The Mitrocystitidae, in particular, had a number of additional resemblances to each of the three extant subphyla, related especially to the cranial nerves and brain and to asymmetries of structure. These resemblances are most unlikely to be coincidental and clearly indicate that the extant subphyla of chordates were descended from Stylophora. It therefore seems just to transfer the Stylophora from the Echinodermata, which they resemble less markedly, to the Chordata. Since the Stylophora have resemblances to all the extant subphyla of chordates, but cannot clearly be placed in one rather than another, and since they also have features that distinguish them as a group from all the extant subphyla, it is reasonable to establish a new subphylum—the Calcichordata—to receive them.

The differences which separate all Stylophora from all extant chordates are the calcite skeleton, the adaptation of the posterior part of the stem for vertical flexion, the abrupt end of the stem which may imply attachment by the stem in the larva, and the probable presence of a longitudinal blood vessel within the notochord. These differences suggest that the other chordates have arisen from Stylophora only once. If this is the case it is the mitrates, and among mitrates the Mitrocystitidae rather than the Lagynocystidae, which were the group from which these other chordates arose, since Lagynocystidae lack the lateralis system (unlike Agnatha and fish) and have the mouth facing somewhat to the right (unlike larval amphioxus). Further, it is probably very primitive mitrocystitids which are in question since the earliest-known agnathans, which are also the earliest-known chordates other than calcichordates, are Lower Arenig in age (Bystrov 1955 : 473), while the earliest-known mitrocystitid (*Chinianocarpus thorali*) is Upper Tremadoc or Lower Arenig. This is supported by the fact that *C. thorali*, more than later mitrocystitids, has a mouth opening strongly to the left.

It should be mentioned that some peculiarities of the peduncular blood system of the Mitrocystitidae particularly studied here, i.e. the dorsal longitudinal blood vessel with interossicular vessels going up to it through the dorsal nerve canal, may have been absent from the earliest Mitrocystitidae since no dorsal longitudinal vessel exists in the Lagynocystidae. Alternatively the dorsal vascular complex may have been lost in subsequent evolution.

It is fairly certain that the Stylophoran calcite skeleton could not have directly given rise to an apatite skeleton because: 1. Calcite cannot gradually be converted to apatite, since there is nowhere in the calcite lattice for the insertion of phosphorus ions. 2. The earliest agnathans were probably either naked or covered with loose denticles or scales, for the Arenig forms are known only as dermal denticles

(Bystrov 1955) or perhaps as fragments of scales (Ørvig 1958 : 4). Middle Ordovician agnathans, also, had skeletons consisting basically of small scales or plates, sometimes fused over the head region. Big plates superficially resembling those of Mitrocystitidae only developed later (Tarlo 1962; Denison 1964). In addition both Cephalaspidae (Westoll 1945 : 345) and primitive Osteostraci (White 1958; Denison 1964 : 459) had long, unossified larval stages. 3. Vertebrate apatite is seeded extracellularly by collagen fibrils with 650 Å repetition (e.g. Glimcher *in Sognnaes* 1960). Echinoderm calcite, and therefore presumably calcichordate calcite as well, is seeded from a tiny calcite crystal in a vacuole, intracellularly (Bevelander & Nakahara *in Sognnaes* 1960). These two processes are totally unlike.

Skeletal calcite was therefore most probably lost in the course of evolution, producing a cartilaginous skeleton resembling that which occurs in some holothurians. An apatite skeleton arose later, by seeding of apatite round the collagen fibrils. This may have happened more than once. It is interesting that the ground-mass of echinoderm calcite, like cartilage, contains abundant collagen fibrils (Randall *et al.* 1952).

The history of the evolution of other chordates from calcichordates may therefore have been somewhat as follows. In the Upper Cambrian, or at latest Tremadoc Series, a population of primitive mitrates which lived in the shallow sea and were most probably mitrocystitids resembling *Chinianocarpus*, took to swimming more and more continuously in a forward direction, like tadpoles, by flexing the anterior part of the stem from side to side.

A member of the population that did this had the rudiments of a lateral-line system, optic, olfactory and trigeminal cranial nerves, a tunicate-vertebrate ultra-structure in its visual cells, and a basically fish-like brain. It also had paired atria, paired gill openings and paired gill slits, with the left gill slits preceding the right ones in ontogeny. The rectum opened into the left atrium. The stem had an abrupt posterior end, indicating that the larva had, for a short time, been attached by the end of the stem. The stem was divided into an anterior, laterally flexing part and a posterior, vertically flexing part. In the stem were segmented muscle blocks, a notochord which ended at the front end of the stem where the brain was sited, a dorsal nerve cord, and paired ganglia located between muscle blocks. A blood vessel probably ran down the middle of the notochord. Because of its unsymmetrical front end, the animal probably rotated round its longitudinal axis as it swam, in which respect it may have differed from later mitrocystitids.

As an adaptation to swimming the skeleton grew lighter by the appearance of connective-tissue-filled spaces. These finally coalesced and calcite disappeared except, perhaps, for particles in the lateralis system (otoconiae), without which, in the absence of any skeleton heavier than water, the lateralis system would scarcely have functioned (Pumphrey 1950 : 12). Any remaining skeletal tissue was soft and collagen-rich and resembled cartilage.

At the same time the anterior part of the stem expanded at the expense of the posterior part, which was less and less used for anchorage and creeping. Finally these functions disappeared, and even larval attachment by the end of the stem

was given up. The previous larval hold-fast therefore remained attached to the stem in the adult, instead of breaking away from it. There thus arose an organ closely resembling a normal, chordate tail.

As further adaptation to swimming, the sense organs and nervous system increased in complexity. The eyes moved forwards, so as to be better placed to see what the animal was swimming towards, and the brain grew longer. The lateral line system spread as a network over the whole body.

The next stage began when these soft-bodied animals again became temporarily attached as juveniles, probably while still in the yolk-feeding stage. Attachment this time took place by cement organs or adhesive papillae near the front end of the body.

One group of such animals gradually extended this period of attachment until, finally, their adults became completely non-motile, lost most of their sense organs, their tails and their brains, developed a coat of tunicin and became urochordates. The tadpole-like larvae of this group also became simplified to some extent, particularly as regards the nervous system, but retained most of the features of the ancestral juvenile stage which much resembled the ancestral adult. One ancestral feature retained by the tadpoles was rotation during swimming.

In other descendants of the animals which had adopted anterior, larval attachment, the period of attachment remained very temporary. Since the adults remained able to swim, further modification of the tail took place, i.e. the ventral spinal roots separated from the dorsal roots and the longitudinal blood vessel migrated ventrally out of the notochord, if this had not happened already. In addition, the anus became external though it still opened leftward.

From the animals so modified, evolution proceeded in two directions. In one population, perhaps as an adaptation to burrowing, the tail somites, notochord and dorsal nerve cord extended forward to the anterior end of the body with the muscle blocks outside the atria. The atria therefore united, and came to open ventrally. This population lost most of its sense organs, including the optic, olfactory and lateralis systems, and the dorsal root ganglia disappeared. In addition, the forward growth of the myotomes eliminated the brain as a rather unfortunate embryological consequence (Newth 1951 : 256). This population also developed nephridia-like excretory organs, unlike those of any other chordates. It retained the leftward-facing larval mouth, the left gill slits that preceded the right gill slits in ontogeny, and the tendency to rotate during swimming of the calcichordate ancestor. Thus arose the Cephalochordata.

From the population that produced the cephalochordates, another group of animals arose. In these, again, the attached phase of the larvae remained temporary, but the adults remained habitual swimmers in water rather than becoming burrowers. They ceased to rotate as they swam, however, which allowed the sense organs to increase greatly in complexity and accuracy. True eyes with lenses were probably evolved at this stage, and parts of the lateralis system sank into the body to function as accelerometers or ears. The bodies of these animals became more symmetrical. The anus became median. Right and left gill slits came to appear at the same time in ontogeny. Kidneys developed. Also, and perhaps more than once, apatite,

seeded by collagen fibrils, produced a hard skeleton. These animals were the vertebrates. In their basic features they already existed in Arenig times.

The foregoing story is admittedly speculative, but differs from previous speculations on the origin of vertebrates in that it starts from a known beginning.

V. CONCLUSIONS

a. *Phyletic and systematic position*

A study of two members of the Order Cornuta Jaekel 1900, *Cothurnocystis elizae* Bather, and *Corthurnocystis curvata* Bather, and two members of the Order Mitrata Jaekel 1918, *Mitrocystella incipiens* (Barrande) *miloni* Chauvel and *Mitrocystites mitra* Barrande, reveals a basically similar anatomy in all. This justifies the placing of Cornuta and Mitrata in a larger group, the Stylophora Gill & Caster 1960, here regarded as a class. It is fairly certain that the Mitrata evolved from the Cornuta, rather than the converse.

The Class Stylophora is more closely allied to extant chordate subphyla than to any echinoderms, and is better placed in the Phylum Chordata than in the Phylum Echinodermata. Since it cannot be allocated to any of the extant chordate subphyla, and has features which distinguish it from these subphyla collectively, it is necessary to establish a Subphylum Calcichordata (Jefferies 1967) to receive the Class Stylophora.

With Gislén (1930), the Calcichordata are here regarded as ancestral to the other subphyla of Chordata. An Upper Cambrian mitrocystitid probably evolved into a soft-bodied, free-swimming form which gave up larval attachment by the end of the stem. This free-swimming form later took to larval attachment by cement organs near the front of the body, and by various modifications gave rise first to the Urochordata and then in turn to the Cephalochordata and Craniata.

b. *Thecal openings*

A large mouth at the anterior end of the theca is present in all four forms studied. In adult *Mitrocystella incipiens miloni* and, to a greater extent, in juvenile *Mitrocystites mitra*, the mouth opened distinctly leftward. This asymmetry was even more strongly marked in the earliest-known mitrocystitid, *Chinianocarpos thoralis*. It can be compared with the leftward-facing mouth of larval amphioxus.

External branchial slits, which had the mechanical structure of outlet valves, were present in *Cothurnocystis curvata* and *Cothurnocystis elizae* on the left, dorsal part of the theca. Internal gill slits were presumably present on both sides in *Mitrocystites mitra* and *Mitrocystella incipiens miloni*. They were separated from paired branchial openings by atria.

The anus in *Cothurnocystis elizae* was external and just left of the stem. The anus of *C. curvata* was also just left of the stem but was internal, opening into the most median gill slits. In *Mitrocystella incipiens miloni* and *Mitrocystites mitra* the anus was likewise internal, opening into the left atrium as in a living tunicate tadpole.

The lateral line was developed just to the right of the stem in *M. mitra* and *M. i. miloni*.

Other thecal openings in *M. mitra* were the openings bringing the optic nerves (n_3) on to the dorsal surface and the lateral pores bringing nerves n_4 and n_5 on to the dorsal surface.

In *M. i. miloni* the optic nerves n_3 were vestigial, and nerves n_4 and n_5 did not open on the dorsal surface.

c. Thecal chambers

The theca of *C. elizae* was divided into buccal cavity, pharynx and anterior and posterior coeloms. These probably also all existed in *C. curvata*, though the separate existence of pharynx and anterior coelom cannot be demonstrated directly in that species.

The theca of *M. i. miloni* and *M. mitra* was divided into buccal cavity, left pharyngeal chamber, that corresponds to the pharynx of cornutes, right pharyngeal chamber, anterior and posterior coeloms and right and left atria.

The form of the right pharyngeal chamber of the two mitrates studied shows that it must have arisen in ontogeny as an outpouching from the left pharyngeal chamber, which implies that right gill slits probably appeared later in ontogeny than left gill slits, as they do in the ontogeny of amphioxus.

The form of the posterior coelom of the two mitrates studied suggests that it arose as an outpouching from the left pharyngeal chamber. Its presumed mode of origin is comparable with that of a tunicate epicardium.

The oesophagus of *M. i. miloni* probably opened into the left pharyngeal chamber near the median line of the theca.

d. The stem

The stem of Calcichordata is interpreted by analogy with the stem of a living crinoid. Both are compared with the tail of a living chordate, with the following suggested homologies: chambered organ = notochord, peduncular nerve = dorsal nerve cord, haemal strand broadly = caudal vessels, aboral nerve centre = brain, aboral nerves to the theca broadly = cranial nerves. In all known Calcichordata the stem has an anterior part that flexed mainly to right or left, a posterior part that flexed mainly in a vertical plane, and a medial part that included a massive element (dorsal styloid in mitrates, ventral stylocone in cornutes). A massive element of this sort must, however, have been lacking in the hypothetical transitional form between cornutes and mitrates.

The posterior stem of cornutes was fundamentally adapted for flexing upwards, and so consists of imbricating dorsal plates and massive ventral ossicles. The posterior stem of mitrates was fundamentally adapted for flexing downwards, so it consists of imbricating ventral plates and massive dorsal ossicles.

The posterior stem of the two cornutes particularly studied reveals direct evidence of segmented muscle blocks, notochord (= chambered organ) and, probably, paired segmental blood vessels. The posterior stem of the two mitrates studied reveals evidence of dorsal and ventral segmental muscle blocks, notochord, dorsal nerve

cord and paired segmental ganglia connected to the dorsal nerve cord and located between muscle blocks. There was probably also a vessel, running down the middle of the notochord, that sent off vessels laterally and dorsally to the muscle blocks, and there was probably a dorsal, longitudinal vessel.

Prof. Ubaghs' comparison between the stem of cornutes and mitrates and the arm of an asteroid must be mistaken since: 1. The plates here held to be dorsal in cornutes and ventral in mitrates, which Ubaghs regards as homologous and representing cover plates, are ill adapted to open outwards, particularly in the cornute *Cothurnocystis curvata* and the mitrate *Mitrocystella barrandei*. 2. If the mutual orientation of cornutes and mitrates here adopted is correct, then Prof. Ubaghs must be mistaken, because in neither group can the impressions on the internal surfaces of the ossicles (ventral in cornutes, dorsal in mitrates) represent the *outside* of a water vascular system. This mutual orientation depends mainly on the disposition of the thecal chambers.

e. *The brain and cranial nerves*

The brain of the two cornutes studied is at the anterior (proximal) end of the stem, like the aboral nerve centre of crinoids. It can be shown to give rise anteriorly to paired median-line nerves, which go under the rectum, and to paired pyriform bodies. The median-line nerves may correspond to the nerves n_0 of mitrates. The pyriform bodies correspond to the like-named bodies of mitrates. Two upward protrusions of the anterior coelom into the pharynx of *C. elizae* may have carried the peripheral ends of optic nerves (n_3 of mitrates) near the dorsal side of the theca. In addition to these features, much more of the cranial nerve complex of mitrates may have been represented by homologous nerves in cornutes but if so, these did not touch the skeleton.

The brain and cranial nerves of the two mitrates studied were extremely complex and fundamentally fish-like in plan. The brain had an anterior, a medial and a posterior part, equivalent respectively to telencephalon, diencephalon plus optic lobes, and medulla plus ventral mesencephalon. The medial part of the brain had an upper, optic portion, and a lower hypophyseal portion. From the posterior part of the brain, paired posterior part nerves (medullary nerves) went off. From the medial part, paired medial part nerves (optic nerves) went off. Medial and posterior part nerves probably joined on each side to form the paired palmar nerves, which must have communicated laterally with the paired pyriform bodies. They gave rise peripherally to paired nerves n_1 to n_5 , which, with the palmar nerves, constitute the palmate complexes.

Other important features of the cranial nerves of the mitrates studied were the peripheral canals of *M. i. miloni*, the corresponding peripheral grooves of *M. mitra*, the paired olfactory openings to the buccal cavity, the lateral-line ganglion which communicated with the lateral line and was situated just behind the right pyriform body, and paired nerves n_0 , near the median line.

By analogy with cephalaspids, which are here interpreted according to Lindström (1949), nerves n_1 of the palmate complexes probably represent the mandibular trigeminal nerves of agnathans; nerves n_2 represent the maxillary trigeminal nerves

of agnathans; nerves n_3 represent the optic nerves; nerves n_4 and n_5 , which innervate the probably sensory peripheral canals or grooves, may possibly represent the sensory field nerves of cephalaspids. The pyriform bodies are probably homologous with the trigemino-profundus ganglia of agnathans. The olfactory system of *M. i. miloni* and *M. mitra* resembled that of Heterostraci and gnathostomatous fish rather than that of cephalaspids. The nerves n_0 may possibly represent the hyo-mandibular branches of the facial nerves of agnathans.

The optic system of *M. i. miloni* was in all its parts degenerate compared with that of *M. mitra*, whose optic nerves (n_3) ended peripherally in little bulbs external to the skeleton, i.e. eyes.

f. *Posture and habits*

The two cornutes studied habitually lay on the ventral side, as suggested by previous authors. They probably pulled themselves backwards by sideways movements of the stem. *C. elizae* was a deposit feeder and *C. curvata* a suspension feeder.

The two mitrates studied also lay habitually on the ventral side, which most previous authors have regarded as uppermost. They probably pulled themselves backwards by ventral flexing of the stem, and may also have been able to swim forwards by lateral flexing of the stem.

g. *Definition of Subphylum Calcichordata* (Jefferies 1967)

= *Class Stylophora* (Gill & Caster 1960)

Primitive chordates with a skeleton made of calcite plates, each of which is a single crystal. Animal clearly divided into a stem and a theca (tail and body). Stem ending abruptly, with a vertically flexing posterior part, a laterally flexing anterior part and an abrupt posterior end, perhaps indicating larval attachment by the stem. Gill slits present, either internal or external, either confined to the left side, or paired. Mouth at anterior end of theca. Buccal cavity, pharynx, anterior and posterior coeloms, and sometimes other chambers, recognisable in the theca. Brain at anterior end of stem, giving rise to paired pyriform ganglia and sometimes a complex of cranial nerves anteriorly. Stem with notochord and muscle blocks, and sometimes demonstrably provided with dorsal nerve cord and segmental ganglia.

Stratigraphical range: Middle Cambrian to Devonian.

Formal definitions of the orders Cornuta and Mitrata would at present be premature.

VI. REFERENCES

- ALLIS, E. P. 1931. Concerning the mouth opening and certain features of the visceral endoskeleton of *Cephalaspis*. *J. Anat.*, London, **65** : 509-627.
- BARRANDE, J. 1887. *Système silurien du centre de la Bohême*. 7. *Cystidéés*, 233 pp., 39 pls. Prague.
- BARRINGTON, E. J. W. 1965. *The biology of Hemichordata and Protochordata*. vi + 176 pp. Edinburgh & London.

- BATHER, F. A. 1913. Caradocian Cystidea from Girvan. *Trans. R. Soc. Edinb.*, Edinburgh, **49** : 359-529, pls. 1-6.
- 1928. *Cothurnocystis*: a study in adaptation. *Paläont. Z.*, Berlin, **7** : 1-15.
- BERRILL, N. J. 1955. *The origin of vertebrates*, viii + 258 pp. London.
- BERTMAR, G. 1959. On the ontogeny of the Chondral skull in Characidae, with a discussion on the chondrocranial base and the visceral chondrocranium in fishes. *Acta Zool. Stockh.*, Stockholm, **40**, 203-364.
- BOHLIN, B. 1941. The dorsal and lateral cephalic fields in Osteostraci. *Zool. Bidr. Upps.*, Uppsala, **20** : 543-554.
- BYSTROV, A. P. 1955. [The microstructure of the shield of Agnatha, the jawless vertebrates from the Silurian and Devonian periods.] p. 468 ff. in Pavlovskii, E. N. (ed.) [*L. S. Berg Memorial Volume*] : 1-562, Moscow.
- CASTER, K. E. 1952. Concerning *Enoploura* of the Upper Ordovician and its relation to other carpoid Echinodermata. *Bull. Am. Paleont.*, Ithaca, **24** (141) : 5-56, pls. 1-4.
- & EATON, T. H. 1956. Microstructure of the plates in the carpoid echinoderm *Paranacystis*. *J. Paleont.*, Chicago, **30** : 611-614, pl. 74.
- CHADWICK, H. C. 1907. *Antedon*. *L.M.B.C. Mem. typ. Br. mar. Pl. Anim.*, London, **15** : 1-47, pls. 1-7.
- CHAUVEL, J. 1941. Recherches sur les cystoïdes et les carpoïdes armoricains. *Mém. Soc. géol. minér. Bretagne*, Rennes **5** : 1-286, pls. 1-7.
- DE BEER, G. R. 1937. *The development of the vertebrate skull*, Oxford, 552 pp., 143 pls.
- DENISON, R. H. 1956. A review of the habitat of the earliest vertebrates. *Fieldiana, Geol.*, Chicago, **11** : 359-457.
- 1964. The Cyathaspididae. A family of Silurian and Devonian jawless vertebrates. *Fieldiana, Geol.*, Chicago, **13** : 309-473.
- DEVILLERS, C. 1958. *Le crâne des poissons*. pp. 551-687 in GRASSÉ, P.-P. *Traité de Zoologie*, vol. 13, fasc. 1. 924 pp. Paris.
- DILLY, N. 1964. Studies on the receptors in the cerebral vesicle of the ascidian tadpole. *Q. Jl microsc. Sci.*, London, **105** : 13-20.
- DIMELOW, E. J. 1959. *Some aspects of the biology of Antedon bifida* (Pennant). Thesis Univ. Reading.
- EAKIN, R. M. 1965. Evolution of photoreceptors. *Cold Spring Harb. Symp. quart. Biol.*, Cold Spring Harbor, **30** : 363-370.
- GARSTANG, W. 1928. The morphology of the tunicata and its bearing on the phylogeny of the Chordata. *Q. Jl microsc. Sci.*, London, **72** : 51-187.
- GEMMILL, J. F. 1914. The development and certain points in the adult structure of the starfish *Asterias rubens* L. *Phil. Trans. R. Soc.*, London (B), **205** : 213-294, pls. 18-24.
- GIGOUT, G. 1954. Sur un hétérostélé de l'ordovicien marocain. *Bull. Soc. Sci. nat. phys. Maroc.*, Rabat, **34** : 3-7.
- GILL, E. D. & CASTER, K. E. 1960. Carpoid echinoderms from the Silurian and Devonian of Australia. *Bull. Am. Paleont.*, Ithaca, **41** (185) : 1-71, pls. 1-10.
- GISLÉN, T. 1930. Affinities between the Echinodermata, Enteropneusta and Chordonia. *Zool. Bidr. Upps.*, Uppsala, **12** : 199-304.
- GOODRICH, E. S. 1917. "Proboscis pores" in craniate vertebrates, a suggestion concerning the mandibular somites and hypophysis. *Q. Jl microsc. Sci.*, London, **62** : 539-554.
- 1918. On the development of the segments of the head in *Scyllium*. *Q. Jl microsc. Sci.*, London, **63** : 1-30.
- 1930. *Studies on the structure and development of vertebrates*. London.
- GRAVE, C. 1921. *Amaroucium constellatum* (Verrill). 2. The structure and organisation of the tadpole larva. *J. Morph.*, Boston, Mass., **36** : 7-91, pls. 1-4.
- 1944. The larva of *Styela* (*Cynthia*) *partita*. Structure, activities and duration of life. *J. Morph.*, Boston, Mass., **75** : 173-188, pl. 1.
- GRAY, J. 1936. Studies in animal locomotion: 4. The Neuromuscular mechanism of swimming in the eel. *J. exp. Biol.*, Edinburgh, **13** : 170-178, pls. 1-3.

- GRAY, J. & SAND, A. 1936a. The locomotory rhythm of the dogfish (*Scyllium canicula*). *J. exp. Biol.*, Edinburgh, **13** : 200-209.
- & — 1936b. Spinal reflexes of the dogfish, *Scyllium canicula*. *J. exp. Biol.*, Edinburgh, **13** : 210-218, pls. 1-2.
- GREGORY, W. K. 1935. Reduplication in Evolution. *Q. Rev. Biol.*, Baltimore, **10** : 272-290.
- 1936. The transformation of organic designs : A review of the origin and deployment of the earlier vertebrates. *Biol. Rev.*, Cambridge, **11** : 311-344.
- 1946. The roles of the motile larvae and fixed adults in the origin of the vertebrates. *Q. Rev. Biol.*, Baltimore, **21** : 348-364.
- HEINTZ, A. 1962. Les organes olfactifs des Heterostraci. Problèmes actuels de Paléontologie (Evolution des vertébrés). *Colloques int. Centre natn. Rech. scient.*, Paris, **104** : 13-29.
- HUNT, O. D. 1925. The food of the bottom fauna of the Plymouth fishery grounds. *J. mar. biol. Ass. U.K.*, Plymouth (n.s.), **13** : 560-599.
- HYMAN, L. H. 1955. *The Invertebrates: Vol. 4. Echinodermata*. 763 pp. New York.
- 1959. *The Invertebrates: Vol. 5. Smaller coelomate groups*, viii + 783 pp. New York.
- JAEKEL, O. 1900. Über Carpoideen, eine neue Klasse von Pelmatozoen. *Z. dt. geol. Ges.*, Berlin, **52** : 661-677.
- 1918. Phylogenie und System der Pelmatozoen. *Paläont. Z.*, Berlin, **3** : 1-128.
- JARVIK, E. 1954. On the visceral skeleton in *Eusthenopteron* with a discussion of the parasphenoid and palatoquadrate in fishes. *K. svenska Vetensk-Akad. Handl.*, Stockholm, **3** (5) 1, 1-104.
- JEFFERIES, R. P. S. 1967. Some fossil chordates with echinoderm affinities. *Symp. zool. soc. Lond.*, London, **20** : 163-208.
- JOHNSTON, J. B. 1905. The cranial nerve components of *Petromyzon*. *Morph. Jb.*, Leipzig, **34** : 149-203, pl. 5.
- JULIN, C. 1904. Recherches sur la phylogénese des tuniciers. Developpement de l'appareil branchial. *Z. Wiss. Zool.*, Leipzig, **76** : 544-611.
- KINGSBURY, B. F. 1926. Branchiomorphism and the theory of head segmentation. *J. Morph.*, Boston, Mass., **42** : 83-109.
- KOWALEVSKY, A. O. 1867. Entwicklungsgeschichte der einfachen Ascidien. *Zap. imp. Akad. Nauk.*, St. Petersburg (7) **10** (15) : 1-19, pls. 1-3.
- 1871. Weitere Studien über die Entwicklung der einfachen Ascidien. *Arch. mikrosk. Anat. Entw.-Mech.*, Berlin, **7**, 101-130, pls. 10-13.
- KERR, J. G. 1919. *Textbook of embryology. Vol. 2. Vertebrata with the exception of Mammalia*, 591 pp. London.
- LANGELÖF, H. P. 1937. Über die Bewegung von *Antedon rosaceus* und ihre nervöse Regulierung. *Zool. Jb. (Abt. Allg. Zool. Physiol. Tiere)*, Jena, **57** : 235-278, pls. 6, 7.
- LINDSTRÖM, T. 1949. On the cranial nerves of the cyclostomes, with special reference to n. trigeminus. *Acta Zool. Stockh.*, Stockholm, **30** : 315-458.
- MARCUS, E. 1958. On the evolution of the animal phyla. *Q. Rev. Biol.*, Baltimore, **33** : 24-58.
- MARTINI, E. 1909. Über die Segmentierung des Appendicularien-Schwanzes. *Verh. dt. zool. Ges.*, Leipzig, **19** : 300-307.
- MATSUMOTO, H. 1929. Outline of a classification of the Echinodermata. *Sci. Rep. Tôhoku Univ.*, Sendai (Geol.) **13** : 27-33.
- NARASIMHAMURTI, N. 1931. The development and function of the heart and pericardium in Echinodermata. *Proc. R. Soc.*, London (B) **109** : 471-486.
- NEWT, D. R. 1951. Experiments on the neural crest of the lamprey embryo. *J. exp. Biol.*, Edinburgh, **28** : 247-260, pls. 3, 4.
- ØRVIG, T. 1958. *Pycnaspis splendens*, new genus, new species, a new ostracoderm from the Upper Ordovician of North America. *Proc. U.S. natn. Mus.*, Washington, **108** (3391) : 1-23, pls. 1-3.
- PUMPHREY, R. J. 1950. Hearing. *Symp. Soc. exp. Biol.*, Edinburgh, **4** : 1-18.
- RANDALL, J. T., FRASER, R. D. B., JACKSON, S., MARTIN, A. V. W. & NORTH, A. C. T. 1952. Aspects of collagen structure. *Nature, Lond.*, London, **169**, 1029-1033.

- REICHENSBERGER, A. 1905. Zur Anatomie von *Pentacrinus decorus*. *Z. wiss. Zool.*, Leipzig, **80** : 22-55, pls. 3-5.
- ROBISON, R. A. 1965. Middle Cambrian eocrinoids from Western North America. *J. Paleont.* Chicago, **39** : 355-364, pls. 50-52.
- ROMER, A. S. 1949. *The vertebrate body*. 643 pp., Philadelphia & London.
- SEELIGER, O. 1892. Studien zur Entwicklungsgeschichte der Crinoiden. *Zool. Jb. (Abt. Anat. Ont. Tiere)*, Jena, **6** : 161-444, pls. 11-22.
- SOGNAES, R. F. (ed.) 1960. Calcification in biological systems. *Publs. Am. Ass. Advmt Sci.*, Washington, **64** : 1-511.
- STENSIÖ, E. A. 1927. The Downtonian and Devonian vertebrates of Spitzbergen. 1. Family Cephalaspidae. *Skr. Svalbard Ishavet.*, Oslo, **12** : 1-391, pl. 112.
- 1958. *Les cyclostomes fossiles ou ostracodermes*. pp. 173-425 in GRASSÉ, P. P. *Traité de Zoologie*, vol. 13, fasc. I. 924 pp. Paris.
- 1963. The brain and cranial nerves in fossil, lower craniate vertebrates. *Skr. norske Vidensk. Akad. Mat. Naturv. Kl.*, Oslo (n.s.), **13** : 1-120.
- TARLO, L. B. H. 1962. The classification and evolution of the Heterostraci. *Acta Palaeont. pol.*, Warszawa, **7** : 249-281.
- & WHITING, H. P. 1965. A new interpretation of the internal anatomy of the Heterostraci (Agnatha). *Nature, Lond.*, London, 206, 148-150.
- UBAGHS, G. 1961a. Un échinoderme nouveau de la classe des carpoïdes dans l'ordovicien inférieur du département de l'Hérault (France). *C. r. hebd. Séanc. Acad. Sci. Paris*, Paris, **253** : 2565-2567.
- 1961b. Sur la nature de l'organe appelé tige ou pédoncule chez les carpoïdes Cornuta et Mitrata. *C. r. hebd. Séanc. Acad. Sci. Paris*, Paris, **253** : 2738-2740.
- 1963. *Cothurnocystis* Bather, *Phyllocystis* Thorall and an undetermined member of the order Soluta (Echinodermata Carpoidea) in the uppermost Cambrian of Nevada. *J. Paleont.*, Chicago, **37** : 1133-1142, pl. 151-152.
- WALLS, G. L. 1942. The vertebrate eye. *Bull. Cranbrook Inst. Sci.*, Bloomfield Hills, Michigan, **19** : 1-785.
- WÄNGSJÖ, G. 1952. The Downtonian and Devonian vertebrates of Spitzbergen, IX. Morphologic and systematic studies of the Spitzbergen cephalaspids. *Skr. norsk Polarinst.*, Oslo, **9** : 1-616, pls. 1-118.
- WATSON, D. M. S. 1954. A consideration of ostracoderms. *Phil. Trans. R. Soc.*, London (B) 238 (652), 1-25.
- WESTOLL, T. S. 1945. A new cephalaspid fish from the Downtonian of Scotland with notes on the structure and classification of ostracoderms. *Trans. R. Soc. Edinb.*, Edinburgh, **61** : 341-357.
- WHITE, E. I. 1958. Original environment of the craniates. pp. 212-234 in WESTOLL, T. S. *Studies on fossil vertebrates*, 263 pp. London.
- WIJHE, J. W. VAN. 1925. On the temporary presence of the primary mouth opening of *Amphioxus* and the occurrence of three post oral papillae which are probably homologous with those of the larvae of ascidians. *Proc. K. Akad. Wet. Amst.*, Amsterdam, **29** : 286-295.
- WILLEY, A. 1894. *Amphioxus and the ancestry of the vertebrates*. 316 pp. New York and London.
- YOUNG, J. Z. 1950. *The life of vertebrates*. 767 pp. London and Oxford.

EXPLANATION OF PLATES

All illustrated specimens of *Cothurnocystis elizae* and *C. curvata* are from the Starfish Bed, Ashgill Series, Girvan, Scotland. All *Mitrocystella incipiens miloni* are from the Schists à Calymènes (Llandeilo Series), Grand Champ de Traveusot, Traveusot, Ille-et-Vilaine, France. The horizons and localities of *Mitrocystella incipiens incipiens*, *M. barrandei* and *Mitrocystites mitra* are given for each specimen.

Standard plate and ventral spike notations e.g. M_{ILD}, D_{OL}, S_{IL} are not explained in the captions.

A = Sedgwick Museum, E = British Museum (Natural History), GSM = Geological Survey Museum, IG = Institut de Géologie, Rennes, MCZ = Museum of Comparative Zoology, Harvard, NM = Národní Museum, Prague.

PLATE I

Cothurnocystis elizae

FIG. 1. E 23137. Latex cast showing interior of gill slits. au = anterior u-plate ; f = flap ; pu = posterior u-plate ; rp = reniform process.

FIGS. 2, 3. E 23157. Latex casts of dorsal and ventral surfaces of juvenile. an = anus ; cp = crestal plate ; stc = stylocone ; str = strut.

FIGS. 4, 5, 6. E 23394. Ventral, dorsal and oblique lateral aspects of latex casts. Note variation in form of ventral stem ossicles in fig. 4, anterior points on ventral spikes in fig. 6. lap = left appendage ; loap = left oral appendage ; rbc = ridge posterior to buccal cavity on right ; roap = right oral appendage ; stc = stylocone ; vo = ventral ossicle without boss ; vob = ventral ossicle with boss.

FIG. 7. E 28657. Latex cast. Dorsal aspect. Note contrast between plates of dorsal integument in the "foot" region generally, in the region just posterior to the branchial slits and in the "ankle" region. adp = antero-dorsal process ; dp = dorsal plate ; f = flap ; rbc = ridge posterior to buccal cavity on right.

FIG. 8. E 23179. Latex cast. Dorsal aspect showing branchial slits. The flaps indicated f have been slightly displaced after death relative to the posterior u-plate.

FIG. 9. E 23352. Latex cast. Anterior aspect of internal surface of posterior marginals cf. Text-fig. 3E. z = point on pharyngo-visceral line (pvl), cf. Text-fig. 4d. pco = posterior coelom.

FIG. 10. E 23705. Latex cast. Dorsal surface. Large individual with circular plates in the dorsal integument of the "ankle" as well as "foot" region. an = anus ; if = imbrication flap of ventral plate of anterior stem.

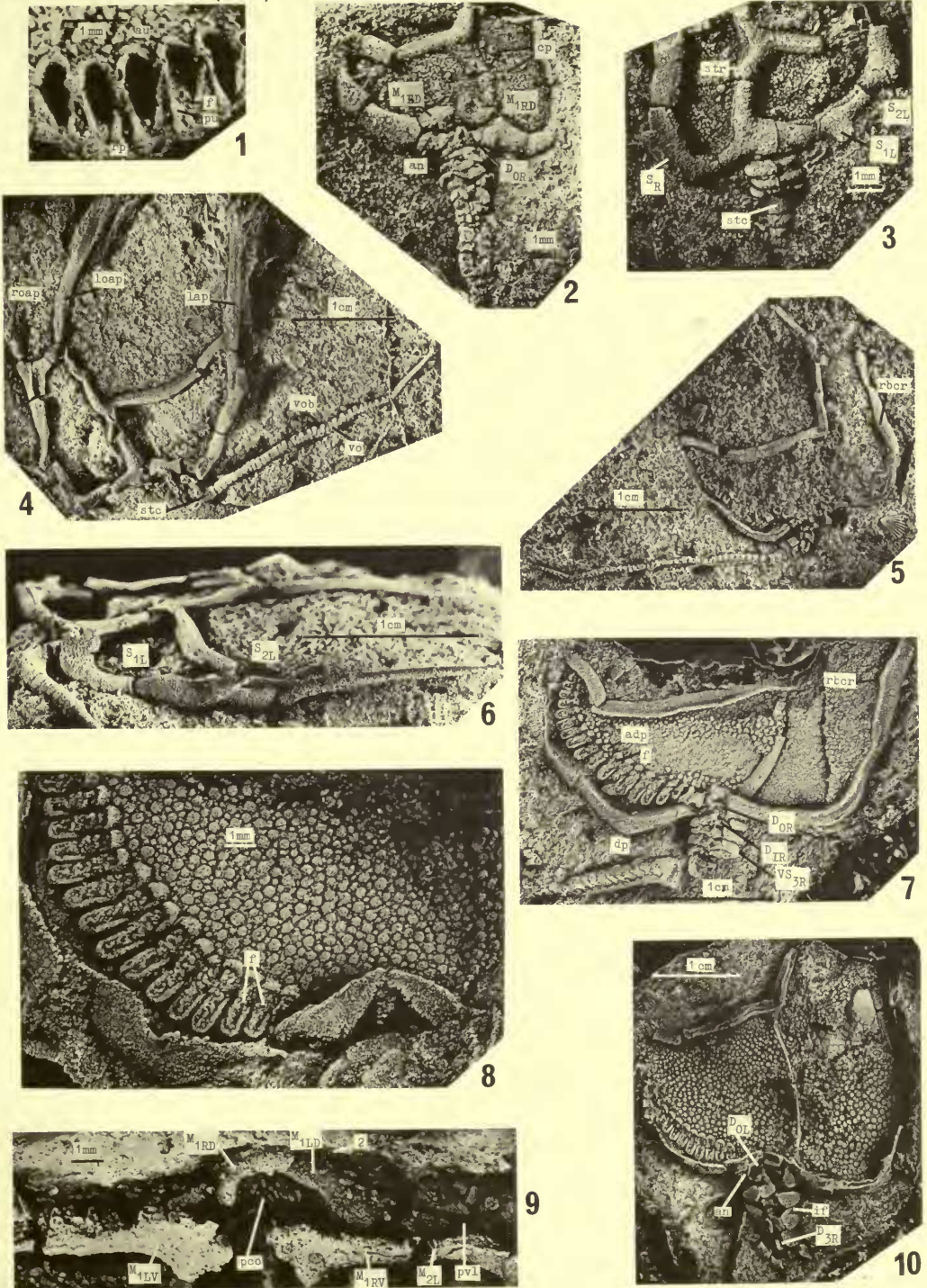


PLATE 2

Cothurnocystis elizae

FIGS. 1, 5, 6, 7. E 28644. Natural mould, ventral aspect. pco = posterior coelom ; rbc = ridge behind buccal cavity on right ; rg = rectal groove. 5, oblique right aspect, ventral side upwards. 6, cast of cerebral basin. 7, posterior coelom, posterior aspect. 4/5, 5, points on pharyngo-visceral line, cf. Text-fig. 4c. mlnl = left median line nerve ; nmln = notch for median-line nerves ; pbl = left pyriform body ; pbr = right pyriform body ; pco = posterior coelom ; pvl = pharyngo-visceral line ; rbc = ridge (on skeleton) delimiting buccal cavity posteriorly on right ; rg = rectal groove (on skeleton) ; sp = striations of pharynx.

FIG. 2. E 28667. Natural mould. Postero-ventral aspect, ventral side upwards. Cf. Text-fig. 4d. 1, 1/2, 3, 3/4, 4, 4/5—points on pharyngo-visceral line. For other letters see explanation to fig. 1, etc.

FIG. 3. E 28660. Latex cast, dorsal aspect. acp = area of circular plates in anterior, left, ventral integument ; rbc = ridge behind buccal cavity on right.

FIG. 4. E 23723. Latex cast. Ventral aspect. Juvenile specimen ; spikes all ill-developed except S_R which is lateral instead of ventral ; articulation at base of right oral appendage (roap) visible. mo = mouth.

FIG. 8. E 28639. Latex cast. Antero-dorsal aspect of inside of theca just anterior to stem. Cf. Text-fig. 3b. gmln = groove for median-line nerve ; hf = horizontal flange of M_{1R+LV} ; nmln = notch for median-line nerves ; pbd = depression for pyriform body ; rg = rectal groove ; rpc = ridge delimiting posterior coelom.

FIG. 9. E 23705. Latex cast. Dorsal aspect of ventral ossicles of posterior stem. Cf. Text-fig. 6. dp = dorsal plate (fragment) ; fdp = facet for dorsal plate ; lpt = lateral pit ; mg = median groove ; tg = transverse groove.

PLATE 3

Cothurnocystis elizae

FIG. 1. E 28639. Latex cast. Dorsal aspect to show right and left internal ridges delimiting the posterior margin of the buccal cavity (rbcl, rbcrl). str = strut.

Cothurnocystis curvata

FIGS. 2, 3, 6. E 28652. 2, dorsal aspect. 3, ventral aspect. 6, anterior aspect. Cf. Text-figs. 7a, b, c. bs = branchial slit ; lap = left appendage ; mo = mouth ; pco = posterior coelom ; rbcl, rbcrl = ridges delimiting buccal cavity on left and right sides ; str = strut.

FIG. 4. E 28662. Dental rubber cast. Ventral aspect of branchial complex. Cf. Text-fig. 9. aep = anterior excavate process ; arc = arcuate canal, formed from apposed arcuate grooves ; pep = posterior excavate process ; vg = ventral groove ; y = point where neighbouring chevrons touch each other, ventral to the arcuate canal.

FIG. 5. E 28652. Latex cast. Same specimen as figs. 2, 3, 6. Dorsal aspect of posterior coelom, the roof of which is incomplete. Cf. Text-fig. 10a.

FIG. 7. E 28551. Latex cast. Ventral aspect. Specimen shows right and left appendages (rap, lap) and supernumary ventral spike (S_{3R}).

FIG. 8. E 23168. Latex cast. Posterior aspect. Cf. Text-fig. 11c.

FIG. 9. GSM 60839. Natural mould. Note distal rectal canal (drc) leaving rectal groove (rg) and opening near the most median branchial slits. bs = branchial slit ; pco = posterior coelom. The branchial skeleton and dorsal integument are represented by moulds of their external surfaces.

FIG. 10. E 28650. Latex cast. Dorsal aspect of anterior stem and region in front of it to show absence of external anus. bs = branchial slit.

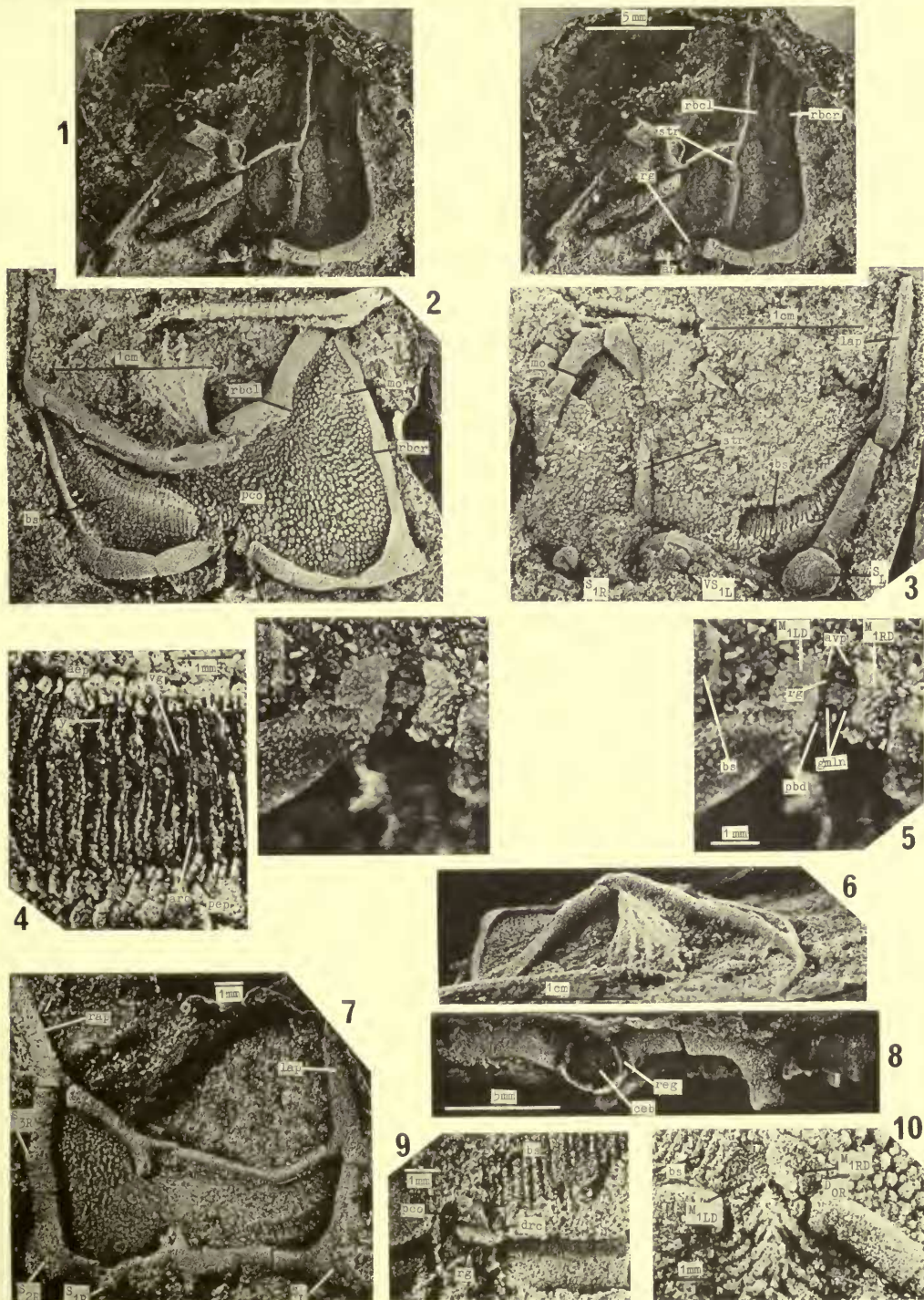


PLATE 4

Cothurnocystis curvata

FIGS. 1, 4. E 28661. Dental rubber cast of posterior stem. 1, right aspect ; 4, dorsal aspect. Cf. Text-fig. 12. admp = admedian process ; afc = anterior facet ; dp = dorsal plate ; mg = median groove ; tb = transverse buttress ; tg = transverse groove. Arrows point towards theca.

FIGS. 2, 3. E 28656. Natural mould of region of buccal cavity, ventral side downwards, to show sculpture on internal mould of theca. 2, left aspect. 3, right aspect. bc = buccal cavity ; liaf = lower integument attachment facet ; uiaf = upper integument attachment facet.

FIGS. 5, 6. E 28572. Natural mould of inside of theca, to show superficial internal sculpture. Ventral side upwards. Cf. Text-fig. 10. 5, posterior aspect. 6, left aspect. ph = pharynx ; liaf = upper integument attachment facet ; uiaf = lower integument attachment facet.

FIG. 7. E 28893. Natural mould of internal cast, anterior aspect. Cf. Text-fig. 10a. liaf = lower integument attachment facet ; ph = pharynx ; uiaf = upper integument attachment facet ; str = strut.

Mitrocystella incipiens miloni

FIG. 8. IG 90. Latex cast. Ventral surface. or = oral plate ; tr = transverse ridge. M_{1RV}, first right ventral marginal.

FIGS. 9, 10. *M. i. miloni*. E 23665. Dental rubber cast. 9, posterior aspect. 10, right aspect. ng = narrow groove (lateral line).

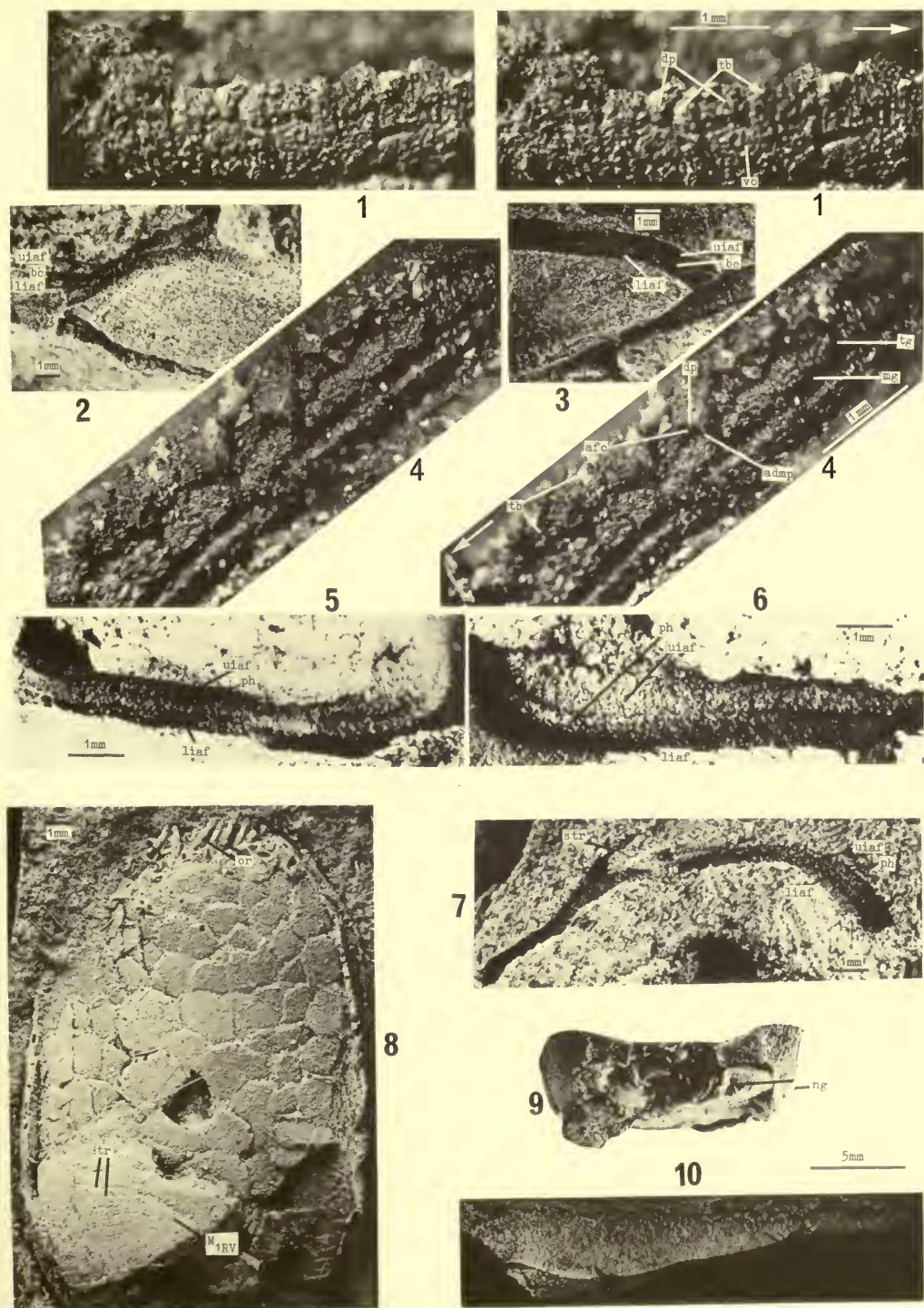


PLATE 5

Mitrocystella incipiens miloni

FIGS. 1, 4. IG 18. Natural mould. 1, dorsal, 4, posterior aspect. gpco = groove limiting posterior coelom ; grp = groove limiting right pharyngeal chamber ; la = left atrium ; lph = left pharyngeal chamber ; n_2 = nerve n_2 of palmar complex ; pal = base of palmar nerve ; pco = posterior coelom ; rb = rectal bridge ; rr = rectal ridge.

FIG. 2. IG 30. Latex cast of dorsal surface. Note calcite cleavage cracks (ccc).

FIGS. 3, 6. IG 110. Natural mould. 3, left posterior part of theca, dorsal aspect. 6, right posterior part of theca, postero-ventral aspect, dorsal side upwards. af = anterior furcation of palmate complex ; csb = carrot-shaped body (lateral-line ganglion) ; e = vestigial eye ; n_{1-5} = nerves of palmate complex ; pal = palmar nerve ; pb = pyriform body ; pc = peripheral canal ; pf = posterior furcation of palmate complex.

FIG. 5. IG 348. Latex cast of posterior stem. Left aspect. ia = interossicular articulation ; do = dorsal ossicle ; vp = ventral plate ; x = point where ventral plate overlaps dorsal ossicle.

FIG. 7. E 28887. Natural mould. Dorsal aspect of anterior part to show buccal cavity (bc) as it appears before dissection cf. fig. 9. n_2 = nerve of palmar complex ; og = oblique groove ; olo = olfactory opening.

FIG. 8. IG 70. Natural mould. The surface shown is a cast of the inside of the external layer of plate M_{1RV} . af = anterior furcation of palmate complex ; csb = broken-off carrot-shaped body (lateral-line ganglion) ; n_{1-5} = nerves of palmate complex ; pal = palmar nerve ; pf = posterior furcation of palmate complex ; pb = pyriform body ; tol = cast of thickening of outer layer of calcite.

FIG. 9. E 23664. Natural mould. Dorsal aspect of anterior part with buccal cavity partly dissected out. Cf. fig. 7. For legend see fig. 7.

Fig. 10. E 23664. Dental rubber cast, representing dorsal posterior skeleton of theca, ventral aspect. To show nature of separation (llpc) between posterior coelom (pco) and left pharyngeal chamber (lph). obr = oblique ridge ; pb = cupule for pyriform body ; rpco = ridge limiting posterior coelom.

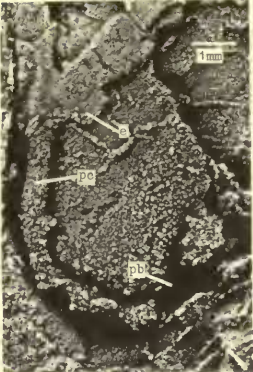
Fig. 11. IG 91. Natural internal mould, ventral aspect of right posterior part. gpco = groove limiting posterior coelom ; n_0 = nerves n_0 ; n_{1-3} = grooves representing nerves of palmate complex ; M_{1RV} = first right ventral marginal plate ; V_{PM} = posterior, median ventral plate (displaced).



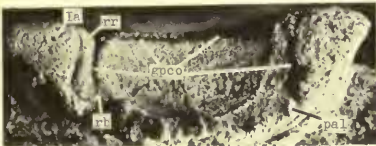
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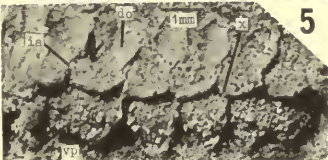
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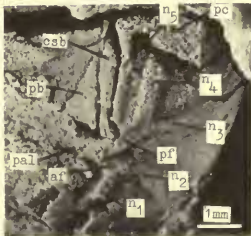
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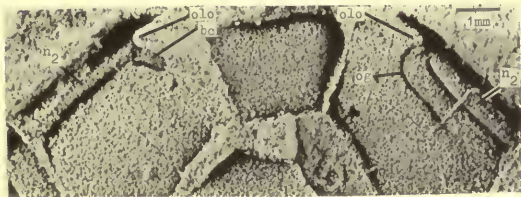
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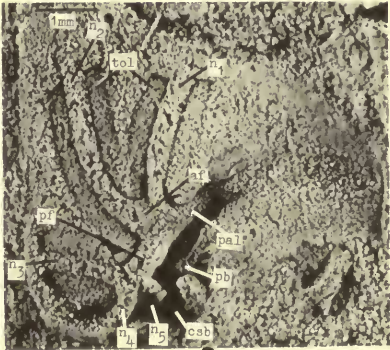
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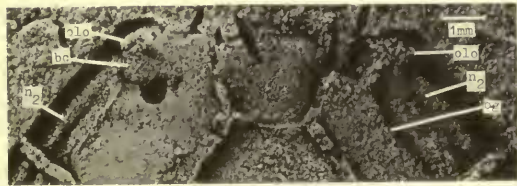
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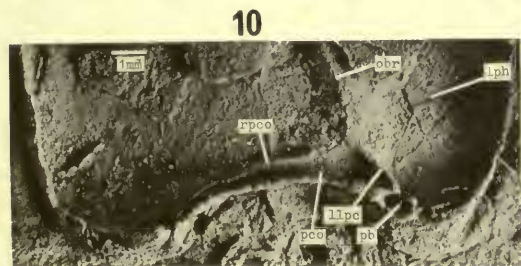
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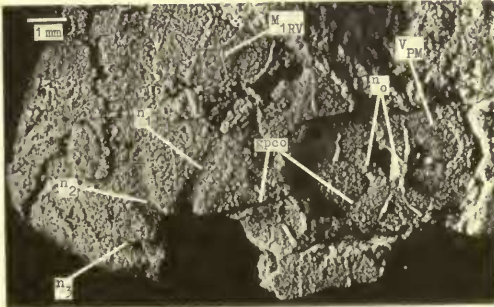
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9



10



11

Mitrocystella incipiens miloni

FIG. 1. A.4627/a. Natural internal mould, dorsal aspect, posterior part. ap = anterior part of brain ; e = eye ; lph = left pharynx ; mp = medial part of brain ; pc = peripheral canal ; pco = posterior coelom ; pp = posterior part of brain.

Mitrocystella barrandei

FIG. 2. NM Akc Kat 437/65. Šarká Beds, Osek Czechoslovakia. Natural mould of cerebral depression representing brain, antero-ventral aspect, dorsal side upwards. lmp = lower medial part of brain (enclosed in life by hypocerebral processes) ; mpf = medial part foramen ; pp = posterior part of brain ; ppn = posterior part nerve ; ump = upper medial part of brain ; w = point of division between lmp and ump.

FIG. 3, 5. E 7517. Šarká Beds, Rokycany, Czechoslovakia. Latex cast. 3, detail of stem, 5, ventral aspect. as = anterior stem ; do = dorsal ossicle ; ia = interossicular articulation ; or = oral plate ; vp = ventral plate ; x = point where ventral plate overlaps dorsal ossicle.

Mitrocystella incipiens miloni

FIG. 4. IG 3. Natural mould representing brain, antero-dorsal aspect. mp = medial part of brain ; mpf = medial part foramen ; ng = narrow groove (lateral line) ; pb = pyriform body ; pp = posterior part of brain ; ppn = posterior part nerve.

Mitrocystites mitra

FIG. 6. MCZ 565. Šarká Beds, Osek. Natural mould, dorsal aspect of posterior part. la = left atrium ; mp = medial part of brain ; n_2 , n_3 , n_{4+5} = nerves of palmate complex ; mp = medial part of brain ; og = oblique groove ; pp = posterior part of brain ; ra = right atrium.

M. i. miloni

FIG. 7. IG 355. Internal cast of M_{1RD} . ccc = calcite cleavage cracks ; pc = peripheral canal ; sc = short canals across $M_{1/2R}$, possibly carrying olfactory fibres.

Mitrocystites mitra

FIG. 8. NM Akc Kat 22011, 1923, 681. Hanuš Colln. 256. Šarká Beds, Šarká, Czechoslovakia. Latex cast. Same specimen as Pl. 10, fig. 4. Dorsal aspect of oral plates. hg = hmiocylindrical groove ; or = oral plates.

FIG. 9. NM Akc Kat. 22011/1923. Šarká Beds, Šarká. Natural mould of anterior surface of posterior stem ossicle. aig = anterior interossicular groove ; aiid = anterior inner interossicular depression ; aoid = anterior outer interossicular depression ; dlc = dorsal, longitudinal canal.

Mitrocystella incipiens miloni

FIG. 10. IG specimen h. Natural mould of ventral side of a dorsal, posterior stem ossicle giving representation of original soft structures. dnc = dorsal nerve cord ; gap = ganglionar process ; lg = lateral ganglion ; not = notochord ; pig = posterior interossicular groove ; popg = post ganglionar process ; z = boundary between dnc and not.

FIG. 11. IG 45. Internal cast of posterior dorsal posterior stem ossicle, right aspect. aiid = anterior, inner, interossicular depression ; aoid = anterior, outer, interossicular depression ; dlc = dorsal longitudinal canal ; mg = median groove infilling (= notochord) ; pig = posterior interossicular groove ; piid = posterior inner interossicular depression ; poid = posterior, outer, interossicular depression.

FIG. 12. A 46271 (same individual as in Pl. 6, fig. 1 and Pl. 7, fig. 3). als = anterior lumen of styloid ; dlc = dorsal longitudinal canal ; vgl = vertical groove on lumen of styloid.

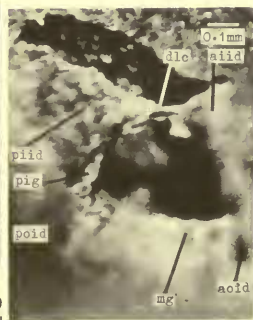
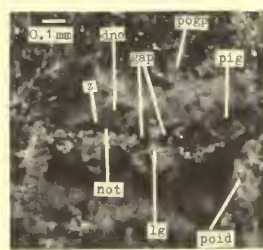
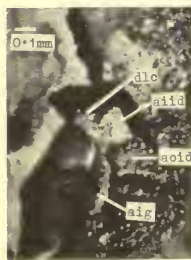
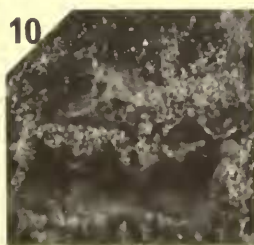
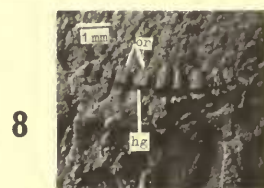
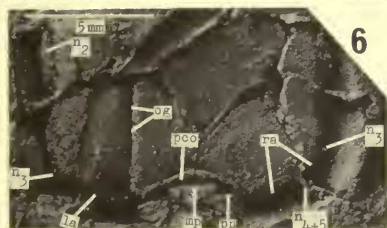
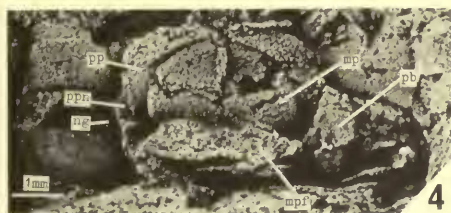
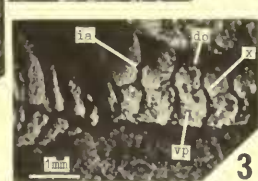
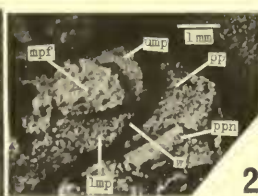
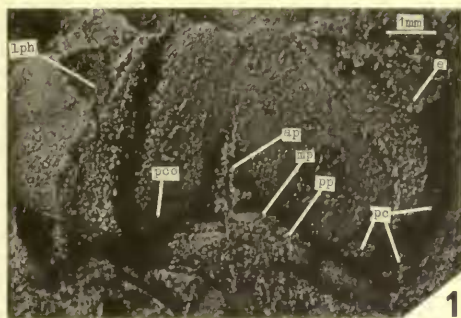


PLATE 7

Mitrocystella incipiens miloni

FIG. 1. E 28889. Trace of palmar nerve (pal) on anterior face of posterior coelom.

FIG. 2. IG 48. Natural mould of ventral side of dorsal posterior stem ossicle immediately behind styloid. Theca right of picture. lga = left ganglion; rga = right ganglion; ic = interossicular canal. For other legends see Pl. 6, fig. 10.

FIG. 3. Internal natural mould of styloid. A 46271. Same specimen as Pl. 6, figs. 1, 12. ic = interossicular canal between fused ossicles of styloid; lg = lateral groove; pig = posterior interossicular groove; piid = posterior inner interossicular depression; poid = posterior outer interossicular depression.

Mitrocystites mitra

FIG. 4. Same specimen as Pl. 6, fig. 9. Internal mould of M_{2L} ; on_3 = opening of n_3 on to dorsal surface; sl = excavation in skeleton for soft layer of skeleton.

Mitrocystella incipiens incipiens

FIG. 5. MCZ 580. Šarká Beds, Svata Dobrotivá, Czechoslovakia. Internal mould of posterior stem. dlc = dorsal longitudinal canal; gmb = groove separating muscle blocks; iid = infilling of interossicular depression; not = notochord; oid = outer, interossicular depression.

Mitrocystella incipiens miloni

FIG. 6. IG 48. Natural internal mould, posterior part, left-dorsal aspect. og = oblique groove; sll = infilling of excavation in skeleton for reception of lateral extensions of ventral soft layer; slp = the same for posterior extensions of ventral soft layer.

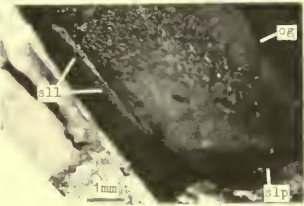
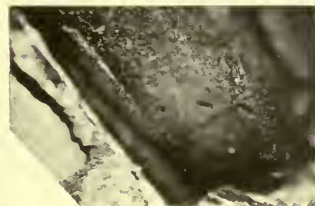
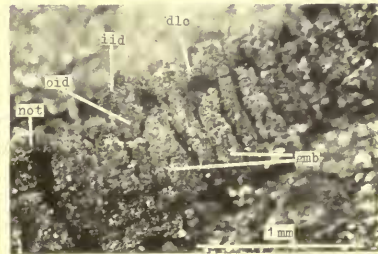
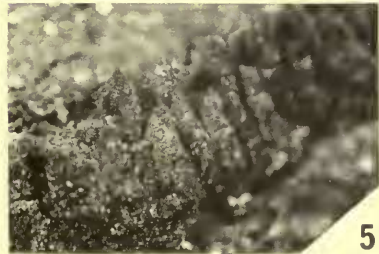
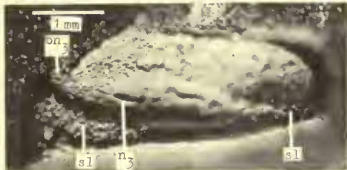
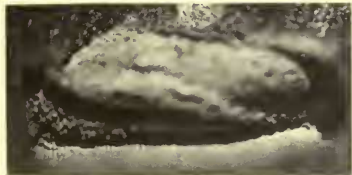
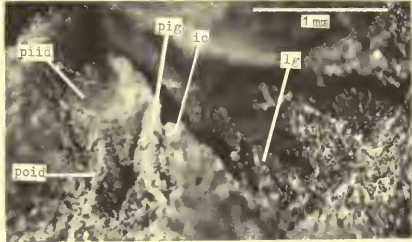
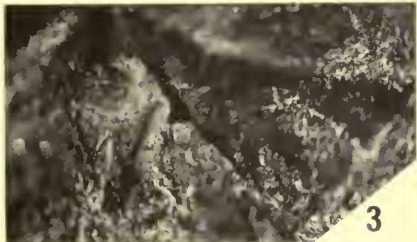
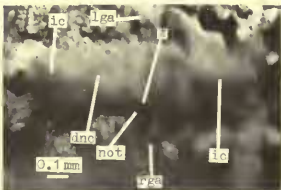
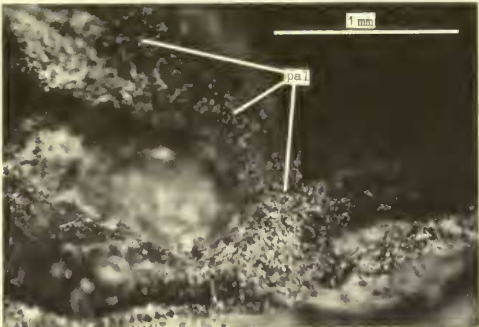


PLATE 8

Mitrocystites mitra

FIG. 1. E 16062. Šarká Beds, Osek, Czechoslovakia. Dental rubber cast, dorsal aspect. dn_3 = depression at end of nerve n_3 (optic depression) ; do = dorsal ossicle ; ia = interossicular articulation ; lp = lateral pore ; pg = peripheral groove ; on_3 = opening of nerve n_3 on to dorsal surface ; std = styloid.

FIGS. 2, 4, 6. MCZ 566. Šarká Beds, Osek. Dental rubber casts. 2, dorsal aspect of M_{1LV} . 4, ventral aspect of posterior left, dorsal skeleton. 6, antero-ventral aspect of the same, dorsal side upwards. af = articular facet ; bo = branchial opening ; bsl = break in slope anterior to af ; gmpn = groove for medial part nerve ; hcp = hypocerebral process ; il = inner layer of skeleton ; la = left atrium ; mpf = medial part foramen ; obr = oblique ridge ; ol = outer layer of skeleton ; pb = cupule for pyriform body ; rpc = ridge delimiting posterior coelom ; $sl(n_{4+5})$ = cavity for soft layer of skeleton carrying nerves n_4 and n_5 .

FIG. 3. NM Akc Kat 22011/1923, Inv. no. 511, Šarká Beds, Šarká. Latex cast. Ventral aspect of posterior part of theca. ng = narrow groove (lateral line) ; bo = branchial opening.

FIG. 5. NM Akc Kat 22011/1923 Hanuš Collection no. 354 +. Latex cast. Ventral aspect of dorsal skeleton. Juvenile specimen showing fenestrated calcite and leftward facing mouth. ceb = cerebral basin ; obr = oblique ridge ; olo = olfactory opening.

FIGS. 7, 9. E 16067. Šarká Beds, Osek. Natural mould of cerebral basin representing brain. 7, anterior aspect. 9, right aspect. ap = anterior part ; mp = medial part ; pp = posterior part ; ppn = posterior part nerve.

FIG. 8. NM Barrande Collection. Osek. Latex cast, ventral aspect. or = oral plate ; por = post oral plate.

FIG. 10. MCZ. 567. Natural internal mould, dorsal aspect. The specimen has been encrusted by a branching epizoan. la = left atrium ; mb = median branch of oblique groove ; mp = medial part of brain ; n_2 = main trunk of nerve n_2 , n_{2A} = anterior branch of nerve n_2 ; n_3 = nerve n_3 (optic nerve) ; og = oblique groove ; olo = olfactory opening ; pp = posterior part of brain ; rr = rectal ridge ; tr = transverse ridge.

PLATE 9

Mitrocystella incipiens miloni

FIG. 1. E 28886. Natural internal mould, dorso-posterior aspect of right half. af = articular facet of M_{1RD} ; csb = carrot-shaped body (lateral-line ganglion); gpco = groove limiting posterior coelom; mpf = medial part foramen; n_5 = nerve n_5 of palmate complex; pb = pyriform body; ra = right atrium; slp = posterior extension of soft layer into dorsal skeleton.

FIG. 2. IG 18. Same specimen as Pl. 5, figs. 1, 4. Latex cast showing oblique ridge near median branch (mb). Between the median branch and the point v, the oblique ridge was probably in contact with the anterior opening of the oesophagus.

Mitrocystella incipiens incipiens

FIG. 3. Same specimen as Pl. 7, fig. 5, but more posterior. Pyritous internal mould of posterior stem. dlc = dorsal longitudinal canal; fdo = fragments of dorsal ossicle ventral to mc; ic = interossicular canal; id = infilling of inner interossicular depression; lbv = lateral blood vessel; mc = infilling of median canal (notochord).

FIG. 4. IG 45d. Natural mould of external surface of M_{1RV} and M_{1RD} showing cruciform lateral line (narrow groove = ng) and part of lateral-line ganglion (carrot-shaped body = csb).

Mitrocystites mitra

FIG. 5. MCZ. 568. Šarká Beds, Osek, Czechoslovakia. Natural mould of ventral surface of dorsal ossicles of posterior stem, giving a representation of the soft parts. dnc = dorsal nerve cord; dvf = dorso-ventral facet, for reception of ventral plate; ic = interossicular canal; lga = lateral ganglion; not = notochord; pig = infilling of posterior, interossicular groove.

FIG. 6. NM Akc Kat 32417/1950. Šarká Beds, Osek. Latex cast of cerebral basin, posterior aspect. lmp = part of basin carrying lower medial part of brain, i.e. inside of hypocerebral processes; mpf = medial part foramen; pp = part of basin carrying posterior part of brain; ump = part of basin carrying upper medial part of brain; w = blunt ridge on skeleton separating ump from lmp (cf. Text-fig. 27b, c, Pl. 6, fig. 62).

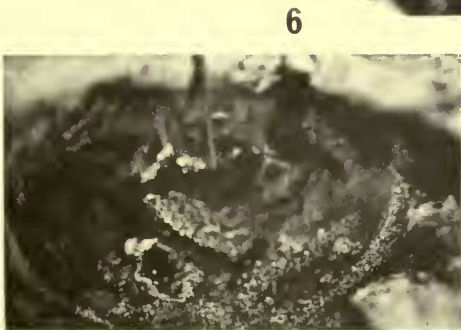
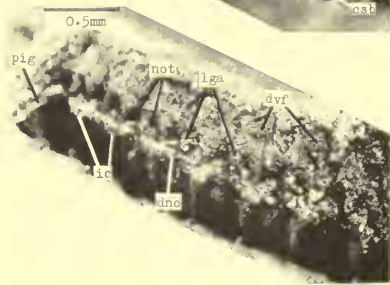
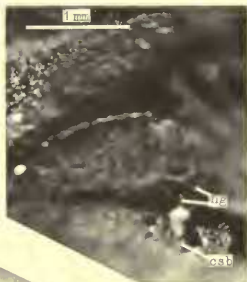
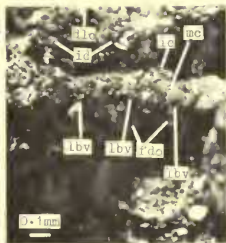
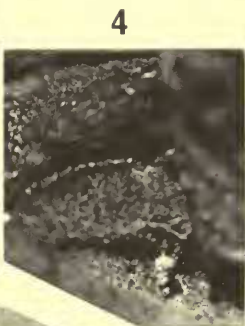
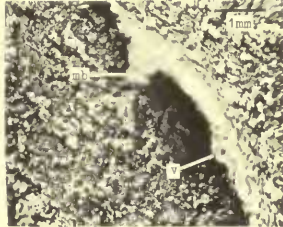
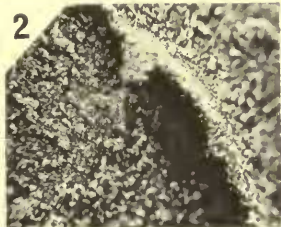
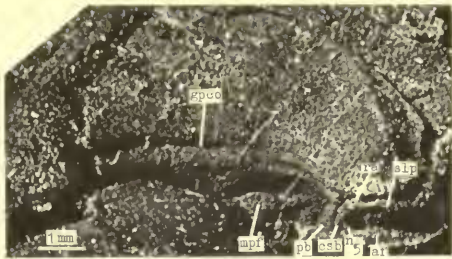
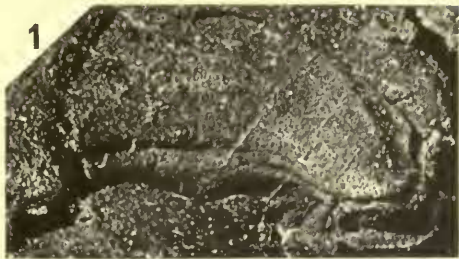


PLATE 10

Mitrocystella incipiens miloni

FIG. 1. E 28888. Note striations (sp) on left pharyngeal chamber. grp = groove limiting right pharyngeal chamber ; n_2 = nerve n_2 ; pco = posterior coelom ; sl = soft layer of dorsal skeleton.

FIG. 2. IG 53. Natural mould. Left dorsal aspect to show typical posture with theca horizontal and posterior stem bent ventralwards. als = anterior lumen of styloid ; as = anterior stem ; ps = posterior stem.

FIG. 3. St. Andrews University, MacGregor Colln. T.3. Natural internal mould of posterior portion of theca, dorsal aspect. csb = carrot-shaped body (lateral-line ganglion) ; csbn = nerve to csb ; n_5 = nerve of palmate complex ; og = oblique groove ; mp = medial part of brain ; slp = posterior extension of soft layer into dorsal skeleton.

Mitrocystites mitra

FIG. 4. Same specimen as Pl. 6, fig. 8. Dorsal aspect of most of ventral and part of dorsal skeleton. il = inner layer of ventral skeleton ; ol = outer layer of ventral skeleton.

FIG. 5. MCZ 566. Šarká Beds, Osek, Czechoslovakia. Latex cast. Dorsal aspect of posterior, dorsal skeleton. Shows finer surface ornament in region of peripheral grooves (pg) than elsewhere. lp = lateral pore ; on_3 = opening of n_3 on to dorsal surface ; tr = transverse ridge.

FIG. 6. E 16058. Šarká Beds, Osek. Natural internal mould of dorsal skeleton, dorsal aspect. Note especially striations of right pharyngeal chamber (sp) and groove (grp) limiting right pharyngeal chamber on the median side. la = left atrium ; mb = median branch of oblique groove ; mp = medial part of brain ; n_2 , n_3 , n_5 , n_{4+5} = nerves of palmate complex ; pco = posterior coelom ; pp = posterior part of brain ; rr = rectal ridge ; tr = transverse ridge.

FIG. 7. E 15017. Šarká Beds, Osek. Latex cast. Dorsal aspect to show stem flexed to right, probably in a fairly natural position. as = anterior stem ; lp = lateral pore ; on_3 = opening of nerve n_3 on to dorsal surface ; pg = peripheral groove ; ps = posterior stem.

FIG. 8. Same specimen as in Pl. 10, fig. 6. Internal mould of posterior part of ventral skeleton. csb = carrot-shaped body (lateralis ganglion) ; gpco = groove limiting posterior coelom ; n_3 = nerve n_3 of palmate complex in ventral skeleton ; pb = pyriform bodies (damaged in dissection) ; sl = soft layer of ventral skeleton.



